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PRAIRIE VEGETATION OF A MOUNTAIN-FRONT AREA IN COLORADO

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(WITH NINE FIGURES)

This account is based on a study, during the past three seasons, of plant associations in the Great Plains region and of their modifications along the mountain-front. These are caused by climatic, physiographic, and vegetational differences which are of influence immediately adjoining the foothills, and to a less degree within a "mesa" belt extending eastward for several miles from the mountains. The study was carried on chiefly in the neighborhood of Boulder, Colorado. The area under particular consideration may be seen in the map (fig. 1). The mesas at Colorado Springs, slightly more arid than those at Boulder, have been studied by SHANTZ (**17**). A mountain-front area in New Mexico has recently been described by WATSON (**20**). Vegetation of the open plains has been studied principally by POUND and CLEMENTS (**13**), and by SHANTZ (**18**).

The region

The structure of the Great Plains is well described by JOHNSON (**10**, especially pp. 627, 628). They are essentially a structural rock slope, covered by débris from the Rocky Mountains. Near the mountains the débris apron is a mixture of rock fragments of all sizes; it has been removed in places by erosion, exposing the shales or sandstones beneath, with their residual soils. The

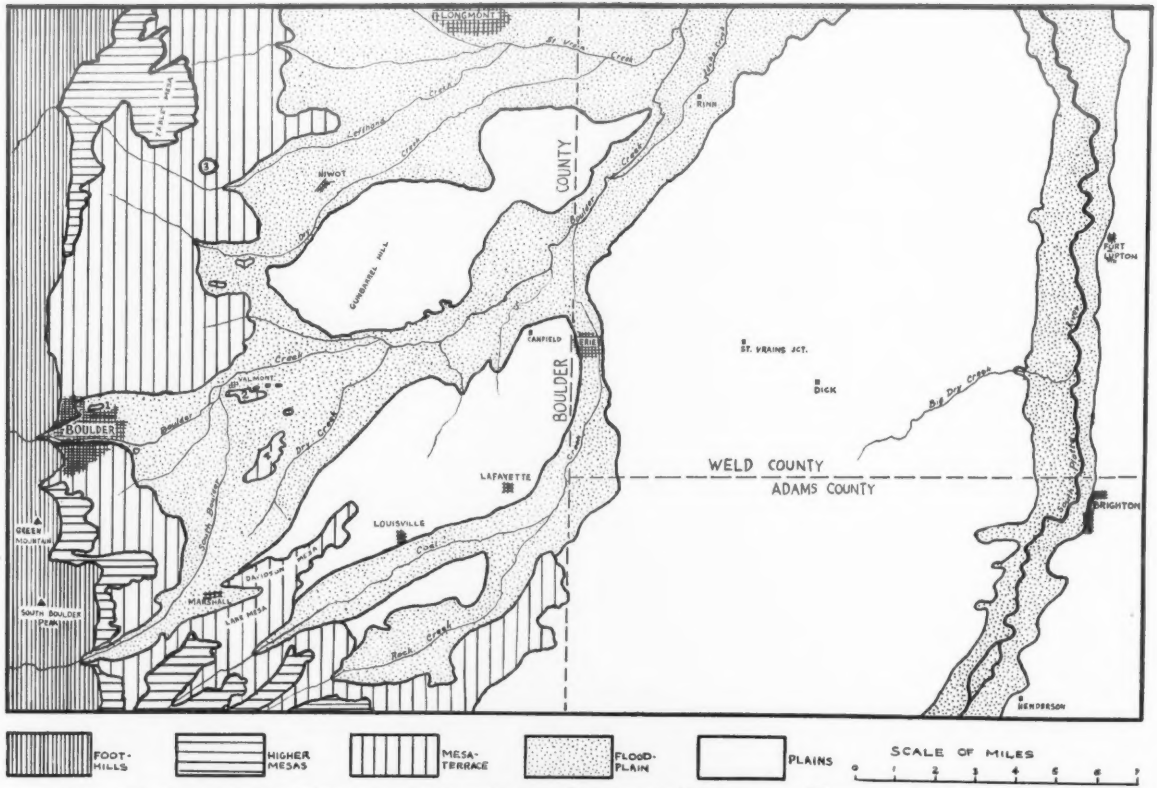

FIG. 1.—Physiographic map of the area studied: a photographic copy of adjoining parts of four sheets of the U.S. Geological Survey topographic atlas was used as a base; the high mesa areas north of Boulder Creek, and those extending east along the lower border of the map, are not exact physiographic counterparts of those between Boulder and South Boulder creeks; they are also drier, and the vegetation is that of the mesa-terrace.

uneroded areas are left as elevated benches, locally called mesas, which have been described by LEE (11) and which are discussed also by FENNEMAN (4) and by DODDS (3). The physiographic divisions of the region are shown in the map (fig. 1); they are as follows:

1. The foothills, with their hogback ridges and upturned crags, locally quite variable in soil, exposure, slope, etc.

FIG. 2.—Green Mountain and its mesas: in the foreground the mesa-terrace level occupied by a modified short-grass growth; next the floodplain of South Boulder Creek; next a continuation of the mesa-terrace; above that the higher mesa level, interrupted, with long slopes, and graded tops partly covered with pines; October 1913.

2. The mesas of the older and higher level, not continuous along the mountain-front.

3. The mesa-terrace, a more extensive, lower, and more recently graded surface.

4. The floodplain, of the present and still lower stream grade, generally débris-covered as the two mesa levels.

5. The plains proper, usually separated from the mountain-front, and with generally fine soil, residual or aeolian.

The first four divisions may be distinguished in fig. 2.

A mesa may abut at its head upon the higher slopes of the foothills or of a mesa of a higher level, or it may be isolated, cut off by

of the map, are not exact physiographic counterparts of those shown
vegetation is that of the mesa-terrace.

erosion. Vegetation of cut-off mesas more closely approximates that of open plains. The physiographic parts of a mesa are four:

1. The mesa-top, flat, slightly inclined (at the angle of the stream gradient), and covered with unassorted rock waste. An exposure of the detritus cap is shown in fig. 3.

2. The mesa-crest, either abrupt, with loosely strewn surface rocks, and coarse, dry, unstable surface soil; or gently rounded, with soil conditions as on the mesa-top.

FIG. 3.—Vertical exposure of the detritus cap of a remnant of mesa-terrace four miles east of Boulder: the layer of mixed soil is about twelve feet deep; the surface layer is darker; the substratum is Fort Pierre shale; 1912.

3. The side-slope, either actively eroding or stable. If the slope has been lowered below the bottom of the mesa-cap, the soil of the slope is usually derived from the substratum, with only a few surface rocks. Otherwise, soil conditions are similar to those of the mesa-top. Seepage areas just below the crest are infrequent.

4. Valleys or draws, originating on the side-slope, usually broad and shallow. Gullies are infrequent. V-shaped ravines, with intermittent streams, are present in the higher mesas. Surface soil is usually fine grained.

Climatic influences within the region have been studied by RAMALEY (14) and ROBBINS (15). Only a brief summary from these two papers is given. Climatic variation from east to west is

probably very abrupt at the mountain-front, although actual data are extremely scanty. The mean annual rainfall at Boulder is 18.46 inches. At Brighton (see map) the annual rainfall is about 4 inches less; on the upper mesa level it is higher than at Boulder. The months of greatest precipitation are April and May. Evaporation is on the whole rapid, less so at the foothills. The mean annual temperature at Boulder is 51° F. Temperature variations are more extreme on the mesa-terrace than on the higher mesas, the plains having a still more severe climate. Temperature inversion is a local factor in reducing diurnal temperature variations in the mesas. The growing season is thus longer at the mountain-front; spring plants appear here several weeks earlier than on the plains some miles to the east.

Diverse character of the vegetation

In the open plains, as discussed by SHANTZ (**18**), the plant associations are well defined, and their relations to soil and topography have been clearly distinguished. Near the mountains, however, associations are more numerous, are variable, mixed in character, not definite. The following conditions are suggested as tending to complicate the character of the vegetation:

1. Climatic conditions undergo a transition at the meeting line of plains and mountain regions. The average climate for the mesa zone, if such a term can be used, is thus intermediate in character.

2. Annual fluctuations in climate are here unusually great, favoring alternately mountain and plains vegetation.

3. Rainfall during April and May is adequate for mesophytic prairie-grass vegetation, while the latter part of the summer is usually dry. Less xerophytic foothill plants are conspicuous in the mesa areas during the vernal period; later, xerophytes of plains and dry prairie-grass predominate.

4. Variability of soil conditions (soil texture, moisture content, run-off, and absorption) is considerable and is extremely local, the usual mesa soil being composed of unsorted rock fragments of all sizes. Mesophytes can grow immediately beside and from under surface bowlders. Local and extreme variability in character of vegetation is thus possible. Radically different plants, as regards growth-form and physiological constitution, occur frequently in the same growth.

5. Topography is considerably and very locally diversified.

6. Opportunity for invasion by mountain plants is very good.

7. Environmental conditions are on the whole severe; the vegetation is in large part open. Open associations are less definite in plant composition than closed associations, in which plant competition has exercised more of a selective influence (cf. footnote below). Different associations are thus as likely to intergrade as to alternate sharply, the more so since environments frequently pass gradually one into another.

8. Present tendencies toward stabilization of mesa vegetation are more or less obscured by artificial factors, chief of which is grazing.

The principal effect of these complicating agencies is the presence of mixed growths of all grades. Mixed associations are frequent, in which plants normally dominating different associations occur together. The various secondary species also are not so regularly associated with particular dominants as would be expected from the study of more nearly typical representations of these same associations in other parts of the prairie region. At present an arrangement of the minor growths and variations of associations must be tentative. The associations are characterized partly from their occurrence and composition in other parts of the prairie province, and while certain growths in the mesa area are typical in composition, the best that can be done at present with certain growths within the area is to regard them as mixtures of two certain associations, or as a representative of one association varying in the direction of another, or with an added plant element from some particular source. On the other hand, certain appearances of some of the associations[1] are quite definite in composition, quite regular and uniform in occurrence in different stations of the mountain-

[1] Definitions of terms applied to plant growths of different rank, as herein used, may conduce to accuracy. The unit of vegetation is taken to be the *plant association*, meaning an essentially uniform assemblage of plants living together in an area essentially uniform in environmental conditions. No interrelationship of different plants is necessarily implied, nor is uniformity taken to exclude internal *local* variability of either environment or vegetation. Those who have worked principally with closed vegetation in the humid eastern states are likely to formulate certain attributes of plant associations which will not apply to open growth in the less favorable environments of semi-arid regions, or to primitive stages in development of vegetation, or to mixed growths in habitats internally variable. In areas of vegetation permanently or temporarily open, plant competition is usually not an important limiting factor; there is no competition for light as in forest, and very little for above-ground space as in closed grassland; root competition is perhaps not so general as accommodation of root systems, so that different plant species derive moisture from different soil depths. Physical conditions may thus exert more direct control upon plant indi-

front, and often definitely to be correlated with particular environmental features.

Synopsis of the associations

The following associations, with the exception of several of the local growths, are typical within, and usually restricted to, the generally treeless interior region of North America, which is characterized by low winter rainfall and grassland vegetation (*Prairie Province*, POUND and CLEMENTS **12**; GLEASON **5**, p. 43). Practically all the associations are considerably variable in composition over their range, which in most cases is extended. No single criterion has been depended upon in classifying the associations.[2]

Associations of extended and general distribution within the area of the province; established vegetation, relatively stable or permanent, occupying the more extensive habitats provided by climate and physiography (Climatic or Major Prairie Associations).

Growth dominated by surface-rooted grasses, extensive in the more arid western part of the province, or Great Plains region.

Dominant plants of low mat form (the short-grass growth-form of grama-grass and buffalo-grass).

Short-Grass Association

Dominant plants taller (wheat-grass); growth extensive in northern parts of the plains region, and extending southward locally along the mountain front. *Wheat-Grass Association*

viduals. It seems advisable at present to make our concept of the plant association quite broad, and to recognize that there are different types of associations.

A *consocies*, as here used, refers to an appearance or representation of an association characterized by one or several of its *dominant* species. English ecologists use *facies* in the sense that consocies is here used. A *society* of an association is taken to mean a representation of an association distinguished by abundance of one or several *secondary* species, using the word secondary to include "principal" and "secondary" species. Certain ecologists would use *society* in the sense that consocies is here used, preferring to use consocies as synonymous with association, reserving the latter term for referring generically to plant growths in general. The writer prefers to distinguish between growths characterized by dominant species and those named for secondary species, by calling the first a consocies, the second a society. It is apparent that there are a number of different kinds of societies. The present use of consocies is that of GLEASON (**5**), who gives criteria (p. 38) for determining whether two growths represent distinct associations or two consocies of the same association.

[2] The associations within a particular region form a complex, which may be classified in different ways, according to the purpose of the study. Bases of classification have been discussed by the writer (Local distribution of grasshoppers in relation to plant associations. Biol. Bull. **25**:150. 1913).

Growth dominated by usually deep-rooted grasses; more extensively developed in the less arid central and eastern parts of the province, or Prairie region, and of local distribution along the mountain-front.

Dominant plants of tuft growth-form (of the *Andropogon* type); many of the secondary species pronounced xerophytes; growth most extensively developed in the central part of the prairie region.

Bunch-Grass Association

Dominant plants close-growing mesophytic grasses, usually sod-formers (of the nature of *Poa pratensis*); secondary species composed of a larger proportion of mesophytes; most extensively developed in the eastern part of the prairie region, particularly along the forest border.

Prairie-Grass Association

Associations of local, though commonly wide, distribution within the area of the province; either established or primitive stages of vegetation; frequently not restricted to the area of the province (Minor Associations).

Associations typical of habitats representing extreme conditions within the area of the province, in which *local* physical conditions, not being in accord with climatic conditions, determine the character of the vegetation to a large extent. The growth is thus as stable and permanent as the physical environment (Local or Edaphic Associations).

Associations of rock or of non-alkaline soils.

Growth of rock surfaces; well developed only in the foothills.

Lichen Association

Associations of dry soil.

In stony or gravelly habitats, as buttes, rock ridges, and exposed mesa-crests.

In the most extremely xerophytic and stony habitats; dominant plants cespitose, prostrate.

Mat Association

In less extreme habitats of coarse or loose soil; dominant plants xerophytic grasses.

Stipa-Aristida Association

In sandy soil; not well represented within the area studied.

Sand-Hills Mixed Association

Associations of soils of high water content.

In moist soils, usually bordering depressions.

Hordeum jubatum Association

In wet or submerged soils.

Swamp Associations, etc.[3]

Associations of saline or alkaline soils.

In deep dry alkaline soil, frequently sandy; growth dominated by tall xerophytic shrubs.

Chrysothamnus-Sarcobatus Association

[3] Swamp associations, dominated by species of *Typha*, *Scirpus*, *Calamagrostis*, *Spartina*, etc., are about the same within the region studied as in other parts of the United States, and are not here discussed.

In clay or loam, sometimes subjected to flooding (margins of reservoirs, alkali flats).

Salt-Grass Association

Associations not typical of particular habitats, but scatteringly distributed chiefly because they are *primitive growths;* early stages in development of vegetation; growths typical of recently denuded or broken surfaces, or of physiographically new environments. Vegetation temporary in character; usually tending to change more rapidly than physical environments (Primitive Associations).

Growth dominated by annuals; short-lived growths typical in recently disturbed areas.

Plains Ruderal Association

Growths dominated by perennials; frequently preceded by a ruderal stage; usually less temporary in character.

Dominant plants xerophytic bunch-grasses.

Primitive Bunch-Grass Association

Dominant plants bushy xerophytes, deep-rooted, not grasses.

Gutierrezia-Artemisia Association[4]

Descriptions of the associations

The descriptions of associations are necessarily brief. Only the very important variations of each association are mentioned, and only dominant or very characteristic plant species receive notice. References to the same growths, or different representations of these same growths, as described by various authors, are given. It is the opinion of the writer that the time has come for correlation of associations in different parts of the same region, in cases in which the region is fairly well known. Effort has been made to select the more important references to prairie associations, but not to make a complete synonymy of the various growths.

THE SHORT-GRASS ASSOCIATION

Buffalo-grass formation.—POUND and CLEMENTS **13**, p. 350.
Bouteloua (grama-grass) formation.—SHANTZ **17**, p. 26.

[4] The *Gutierrezia-Artemisia* association, while most frequent in gravelly mesa-tops, is a primitive growth rather than an association of this particular habitat. In such situations the growth normally develops into short-grass. On the other hand, certain appearances of the *Stipa-Aristida* association (the wire-grass association of SHANTZ, see p. 394), may be, following conditions of disturbance, a primitive association. Local associations, or growths relatively permanent in extreme habitats, may become primitive or temporary associations in the less extreme habitats in which climatic associations are dominant except for a short time after disturbance. Though primitive and local associations cannot always be rigidly separated, it seems helpful to distinguish the two groups.

Grasslands of the high plains.—BRAY 1, p. 91.

Grama-buffalo-grass association.—SHANTZ 18, p. 24.

Grama-grass association.—SHANTZ 18, p. 21.

Grama-grass formation.—HARSHBERGER 7, p. 537 (after POUND and CLEMENTS).

Buffalo-grass formation.—HARSHBERGER 7, p. 528 (after POUND and CLEMENTS).

The short-grass association in its typical form (*Bouteloua-Buchloe* consocies), as developed on the open plains, has been well described by SHANTZ (18). The eastern half of the Boulder region is covered principally by this growth. Near the mountains the buffalo-grass (*Buchloe dactyloides* [Nutt.] Engelm.; *Bulbilis dactyloides* [Nutt.] Raf.) is very scantily represented, as also in the northern part of the plains region. Its scarcity is made up by increased abundance of the grama-grass (*Bouteloua oligostachya* [Nutt.] Torr.), which dominates much of the area. It forms either a pure or nearly pure growth (*Bouteloua* consocies), or, in the coarse soil of the mesa-terrace, enters into a mixed growth (*Bouteloua* mixed consocies). This growth is characterized by abundance of the deeper-rooted perennial plants of the plains region, as *Euphorbia robusta* (Engelm.) Small, *Psoralea tenuiflora* Pursh, *Aragallus Lambertii* (Pursh) Greene, and *Grindelia squarrosa* (Pursh) Dunal; and usually there are additional vegetational and floristic elements: (1) some few deeper-rooted grasses; (2) tall composites, legumes, etc., typical in the more xerophytic prairie-grass just east of the plains region; and (3) less xerophytic plants from the foothills (species of *Pentstemon* and *Mertensia*, *Eriogonum umbellatum* Torr., *Geranium Parryi* [Engelm.] Heller, etc.). Certain of these, as the last two, are rarely found except at the base of surface rocks. Here also are found occasional bunch-grasses, and shrubs from the foothills, as *Ceanothus*, *Prunus*, *Oreobatus*, marking invasion of foothill shrub associations. The vegetation of the mesa near Colorado Springs, described by SHANTZ (17) is in large part to be assigned to the *Bouteloua* mixed consocies. A rather dry representation of this growth is seen in the foreground of fig. 2.

The different growths dominated principally by *Bouteloua* are considered to be parts of the same association, rather than different associations, for the resemblances appear to be more constant and

striking than the differences. The *Bouteloua* mixed consocies, presenting the most radical departure from the typical short-grass growth, is different mainly in the possession of a derived element. Local patches of pure short-grass are still present, and the mesophytic plants are found in very local spots differing in moisture conditions, due to the extreme mixture of all sizes of soil constituents.

FIG. 4.—Wheat-grass, with *Artemisia aromatica* (the dark plant) in fine-grained soil of the mesa-terrace just south of Boulder; June 1913.

THE WHEAT-GRASS ASSOCIATION

Wheat-grass association.—SHANTZ **18,** pp. 21, 48.
Agropyron formation.—POUND and CLEMENTS **13,** p. 383.
Agropyron occidentale consocies.—SHANTZ **17,** p. 36.
Agropyron growth of prairie crests.—HARVEY **8,** p. 279.

The wheat-grass (*Agropyron Smithii* Rydb.; *Agropyron occidentale* Scribn.) is established in rather looser clay soil than that in which the short-grasses dominate. The typical habitat is the deposition area at the base of side-slopes of mesas, with fine soil washed down from above. Recently disturbed clay and what appear to be areas of wind deposition are also occupied by wheat-grass. Invasion by grama-grass is often initiated, and the intermediate

growth in which *Agropyron* and *Bouteloua* occur together is frequently seen. In the pure wheat-grass, *Astragalus goniatus* Nutt. and *Artemisia gnaphalodes* Nutt. together form one very definite society, while *Tium Drummondii* (Dougl.) Rydb. (*Astragalus Drummondii* Dougl.) characterizes a second. A third (fig. 4) is marked by *Artemisia aromatica* A. Nels. *Carex stenophylla* Wahlenb. and *C. pennsylvanica* Lam. dominate very small areas, usually within the wheat-grass association.

The wheat-grass association has very general distribution in northern parts of the Great Plains region, extending locally southward along the foothills. These interrupted growths would probably occupy a much larger area but for the influence of grazing, which appears to favor succession of wheat-grass by grama-grass.

THE BUNCH-GRASS ASSOCIATION

Bunch-grass association.—SHANTZ **18,** p. 54. Eastern Colorado.

High prairie.—HALL **6,** pp. 30–35, in part. Eastern Kansas.

Andropogon-Sorghastrum growth.—HITCHCOCK **9,** p. 64. Eastern Kansas.

Bunch-grass formation.—POUND and CLEMENTS **13,** p. 354. Nebraska.

Grasslands of the semi-humid black-soil prairies.—BRAY **1,** p. 86, in part. Texas.

Andropogon growth of ridges, etc.—HARVEY **8,** pp. 287, 288. South Dakota.

Bunch-grass association.—GLEASON **5,** p. 47, in part. Illinois.

Dry prairies of the prairie-grass formation.—HARSHBERGER **7,** p. 523 (after BRENDEL **2,** p. 34). Central Illinois.

Bunch-grass formation.—HARSHBERGER **7,** 532 (after POUND and CLEMENTS). Nebraska.

The bunch-grass association, though occupying a very small part of the area studied, appears to be similar in composition to bunch-grass growths over the extent of the prairie province. It is best seen near the outer ends of the tops of the higher mesas south of Boulder (mixed bunch-grass consocies). The soil is gravelly, the growth somewhat open, about 35 per cent of bare surface being exposed. A number of species dominate together, in about the following order of importance: *Andropogon scoparius* Michx., *Koeleria cristata* (L.) Pers., *Andropogon furcatus* Muhl., *Sorghastrum nutans* (L.) Nash, *Muhlenbergia gracilis* Trin., *Atheropogon curti-*

pendulus (Michx.) Fourn. (*Bouteloua curtipendula* [Michx.] Torr.). Secondary species include other grasses, rather xerophytic prairie perennials, as *Liatris punctata* Hook., *Gaillardia aristata* Pursh, *Psoralea tenuiflora* Pursh, *Aster Porteri* Gray, and *Chrysopsis villosa* Nutt. The growth is shown in fig. 5.

The bunch-grass association depends upon a constant water supply which endures through the latter part of the summer. As available soil moisture is constantly present in mesa-terrace

FIG. 5.—Bunch-grass at the south crest of Horse Mesa (of the higher level): *Andropogon, Sorghastrum, Artemisia, Carduus;* next to the large rock a shrub of poison ivy; on rock surfaces, lichens; September 1913.

soils only till the middle of July, the association is limited to moist slopes, the higher mesa-tops, and small depressions. Scattered bunch-grasses occur beside surface rocks in the mesa-terrace.

The *Andropogon furcatus* consocies is a pure or nearly pure growth of the big blue-stem. It is found in local areas of coarse soil. There is also the *Andropogon scoparius* consocies, which is synonymous with the bunch-grass association of SHANTZ (**18,** p. 54). The occurrence of a practically closed bunch-grass growth, made

up of *Andropogon furcatus* and *Sorghastrum nutans*, in fine-grained moist soil of stream bottoms in the floodplain, should also be noted.[5] It probably formerly occupied considerable areas.

THE PRAIRIE-GRASS ASSOCIATION

Prairie-grass formation.—POUND and CLEMENTS **13**, p. 348, in part.
Prairie-grass formation.—SHANTZ **18**, p. 23, in part.
Prairie-grass formation.—HARVEY **8**, in part.
Prairie-grass formation.—HARSHBERGER **7**, pp. 522, 527, in part.
Prairie-grass associations.—VESTAL **19**, pp. 354, 355.

The prairie-grass growth within the region is mesophytic, meadow-like, in spring, becoming quite dry in late summer, most of the plants being then dead. It is typically developed in rich black soil of fine texture, of high moisture content in spring and early summer. Such soil is regularly found in alluvial lower slopes of foothills and higher mesas.

The *Poa-Koeleria* consocies is dominated by *Poa Buckleyana* Nash and by *Koeleria cristata* (L.) Pers. *Stipa viridula* Trin., *Poa pratensis* L., *Agropyron violaceum* (Hornem.) Vasey, and *Agropyron Smithii* Rydb. are occasionally present. The growth is tall and close. In alluvial fans at the base of certain slopes, facing to the north usually, the *Arnica* society of the prairie-grass growth is developed (fig. 6). It is characterized by abundance of *Arnica monocephala* Rydb. (*Arnica fulgens* Pursh, in part). The *Delphinium-Cerastium* society is a growth in which *Delphinium Nelsonii* Greene and *Cerastium campestre* Greene are very conspicuous. There are several other well defined societies.

The *Stipa viridula* consocies is dominated by *Stipa viridula* Trin., with occasional other grasses. It is usually on the outer

[5] The occurrence of bunch-grass in such different habitats as its mesa and floodplain stations bears out the view that the plant growth itself, rather than the habitat, should be used in delimitation of associations within even such a small area as the one studied. The resultant conditions essential to the plant growth, that is, continually available moisture, are fulfilled in both situations. SHANTZ has shown (**18**, p. 55) that the *Andropogon scoparius* consocies is found in gravelly soil near the mountains, in sand and loose loam in eastern Colorado, in Fort Pierre clays in South Dakota, and in loam soil in the eastern part of the prairie region. Probably the vegetation itself is a very good expression of the *resultant* of climatic, local, and historic factors; the *complete* environment.

slopes of the foothills. Narrow zones of this growth are frequently found bordering *Symphoricarpos* and *Prunus* shrub associations of the foothills, which appear to be increasing in area on the slopes, at the expense of the grassland. In such meadow-like zones are seen *Frasera speciosa* Griseb., *Thermopsis divaricarpa* A. Nels., *Achillea lanulosa* Nutt., and *Aster Geyeri* (Gray) Howell, with other conspicuous mesophytes. Such meadow-like zones border scrub

FIG. 6.—Society of *Arnica*, in a prairie-grass growth of moist alluvium at the base of a steeper slope, south of Boulder; dominant plants are *Poa* and *Koeleria;* May 1913.

oak associations farther south, at Castle Rock, Perry Park, near Larkspur, and at Palmer Lake.

The prairie-grass locally found west of the plains belt has many features in common with eastern black-soil prairie as represented along the border of the eastern deciduous forest. The secondary species, however, are mostly different, and the growth found along the mountain-front would probably be considered a separate association, which may be called the western mesophytic prairie-grass

association. It may perhaps intergrade with the prairie-grass of the middle part of the prairie region. The growth on what is called the Middle Mesa (fig. 7) is intermediate between short-grass and prairie-grass; it is floristically quite like the South Dakota prairie-grass described by HARVEY (**8**). This similarity is more evident in late summer, xerophytic prairie-grass species

FIG. 7.—Mixed growth of the Middle Mesa, on the outskirts of Boulder: *Koeleria, Stipa, Helianthus, Senecio* (the flat-topped heads), *Erysimum, Aragallus, Eriogonum alatum* (the tall dead stalk), *Eriogonum umbellatum;* in the middle ground, the valley of Boulder Creek (the trees are planted in the town); above, the foothills, generally grass covered, with scattered rock pines, which are more abundant on the rocky ridges; June 1, 1913.

like *Solidago rigida* L., *Sideranthus spinulosus* (Pursh) Sweet, *Helianthus, Petalostemon*, and *Aster* spp. being very conspicuous. The dominant grasses are the same in both Colorado and South Dakota areas. The dry prairies in east and west show considerable similarity; the more mesophytic prairies of east and west show considerable divergence, so far as species composition is concerned.

THE LICHEN ASSOCIATION

Lichen formation.—SHANTZ **17,** p. 188.
Lichen formation.—SHANTZ **18,** pp. 22, 62.

The lichen growth on rock surfaces contributes an element to the vegetation of detrital soils of the higher mesa and mesa-terrace levels within the region. Surface rocks are present on practically all the mesa-tops. The dominant species, as given by SHANTZ (**17, 18**) are *Parmelia conspersa* (Ehrh.) Ach., *Rinodina oreina* (Ach.) Mass., *Lecanora calcarea* (L.) Nyl., and *Lecanora subfusca allophana* Ach.

THE MAT ASSOCIATION

Mat formation of buttes and cliffs.—POUND and CLEMENTS **13,** p. 376.
Mat formation of buttes and cliffs.—HARSHBERGER **7,** 535 (after POUND and CLEMENTS).

The open growth of dwarfed perennials which occupies sterile gravelly stations should perhaps not be regarded as a separate association; it is, however, distinctive in growth-form, and is frequent and well defined on buttes and hogbacks of northeastern Colorado, eastern Wyoming, and western Nebraska. It is physiologically similar to the *Bouteloua hirsuta* growth, and to the *Artemisia frigida* consocies, sometimes being found with these (fig. 8), not, however, in extreme conditions of coarse soil and exposure to sun and wind, as on certain abrupt mesa-crests. A number of the species are found also in gravel slide growths of the mountains. These growths have been studied by CLEMENTS, and by SCHNEIDER (**16**), and are akin to the mat growths of stony habitats of the plains, in several respects.

Distinctive plants of the mat association are: *Townsendia exscapa* (Rich.) Porter, *Orophaca tridactylica* (Gray) Rydb. (*Astragalus tridactylicus* Gray), *Lesquerella montana* (Gray) Wats., *Paronychia Jamesii* T. and G., *Hymenopappus filifolius* Hook., *Gilia pinnatifida* Nutt. Several species of *Chrysopsis*, *Geranium Parryi* (Engelm.) Heller, *Oreocarya virgata* (Porter) Greene, and *Phacelia heterophylla* Pursh are frequently present.

THE STIPA-ARISTIDA ASSOCIATION

Stipa formation of high prairies.—POUND and CLEMENTS **13**, p. 381.
Wire-grass association.—SHANTZ **18**, p. 48.

The dominant plants of this growth are xerophytic grasses of tuft growth-form, with moderately deep roots. They are found usually in coarse sterile soil, more commonly on south-facing slopes and crests.

FIG. 8.—Primitive grassland on a gravelly terrace left by Gregory Creek, which lies across the picture in a slanting position, and is marked by the large tree, a narrow-leaf cottonwood; the growth consists of *Bouteloua hirsuta*, *Artemisia frigida*, and a few mat plants, and is very open; July 1913.

The *Stipa comata* consocies, dominated by *Stipa comata* Trin. and Rupr., occurs in the region on gravelly slopes and on wind-swept tops and crests of mesas. In it are occasionally found *Chrysopsis villosa* Nutt., *Psoralea tenuiflora* Pursh, *Helianthus pumilus* Nutt., *Aristida longiseta* Steud., and *Sitanion brevifolium* J. G. Smith. A pure growth of *Stipa* has been seen on a pebbly railroad embankment.

The *Aristida longiseta* consocies is dominated by the wire-grass (*Aristida longiseta*). It is important (in sandy loam and broken soils) in parts of eastern Colorado and west-central Kansas and Nebraska (SHANTZ **18,** p. 48). In the mesa area *Aristida* does not occur except in association with other grasses, chiefly *Stipa comata*. For the present the two growths have been considered together, on account of similar habitat preference, similarity of secondary species, and regularity of occurrence in association, at least in the region studied. More extended study may show the two growths to be representatives of different associations, which intergrade within the region.

THE SAND-HILLS MIXED ASSOCIATION

Sand-hill formations.—POUND and CLEMENTS **13,** p. 352, in part.
Sand-hills mixed association.—SHANTZ **18,** p. 58.

Within the region studied no truly sandy areas of any extent have been found. Local areas of sandy soil occur with sandstone outcrops and in certain dry stream beds of the plains. The sand-hills mixed association is perhaps not typically developed within the area, though well shown on sandy bluffs of the South Platte at Globeville, on the outskirts of Denver; the usual growth may be referred either to a variation of the short-grass mixed association, or to a primitive open growth made up chiefly of plant species abundant in sand-hills. Sandy soil may be recognized by the presence, often in abundance, of *Mentzelia nuda* (Pursh) T. and G., *Abronia fragrans* Nutt., *Cleome serrulata* Pursh, and *Artemisia filifolia* Torr. *Yucca glauca* Nutt. is often extremely abundant in sandy soil.

THE HORDEUM JUBATUM ASSOCIATION

A pure growth of the squirrel-tail grass (*Hordeum jubatum* L.) typically occupies moist soil of depressions, or a zone of moist soil, of variable width, surrounding swampy areas or standing water, or bordering gently sloping ditch banks. The growth appears to be native in such situations, and geographically widespread.

THE CHRYSOTHAMNUS-SARCOBATUS ASSOCIATION

Chrysothamnus growth of the sage-brush formation.—POUND and CLEMENTS **13,** p. 372.

Greasewood-white sage formation.—POUND and CLEMENTS **13**, p. 374.
Chrysothamnus graveolens society.—SHANTZ **17**, pp. 41, 47.
Bigelovia association.—WATSON **20**, p. 200, in part.
Greasewood society of the *Bigelovia* association.—WATSON **20**, p. 202.

This growth occurs in deep alkaline soil which is usually more or less loose or sandy. *Chrysothamnus graveolens* (Nutt.) Greene (rabbit brush) is more abundant in loam; *Sarcobatus vermiculatus* (Hook.) Torr. (greasewood) is more abundant in sandy loam or sand; the two often dominate together. The lower slopes of the two Table Mountains at Golden are covered with a *Chrysothamnus* growth. *Sarcobatus*, with or without *Chrysothamnus*, is abundant in sandy stream bottoms farther south in the valley of the Arkansas River. With *Chrysothamnus graveolens* are often found *Eurotia lanata* (Pursh) Moq. and *Chrysothamnus plattensis* Greene. An open growth of the latter, usually mixed with the short-grass cover, is frequent in low ground of draws, in which the soil is fine-grained and with a high proportion of soluble salts, or on level alkaline loose clay.

Within the Boulder area these growths are local, and not particularly well developed. They range locally through the plains region, and with similar growths, through the southwestern United States. The present arrangement in one association of the particular growths seen is tentative.

THE SALT-GRASS ASSOCIATION[6]

Salt-grass *Orache* formation.—POUND and CLEMENTS **13**, p. 388, in part.

Two grasses, *Sporobolus asperifolius* (Nees and Mey.) Thurb. and *Distichlis spicata* (L.) Greene, either together or singly, are dominant plants in flats which are sometimes white with alkali. Within the region such flats occur on gently sloping margins of floodplain lakes and irrigation reservoirs, and in restricted stream bottom areas. Irrigation, as at present practised, tends to increase their number and extent. The soil may be clay or loam, is compact, often trampled by cattle, and frequen tly subject to occasional flooding.

[6] Vegetation of saline basins in the prairie region is discussed by J. H. SCHAFFNER in Notes on the salt-marsh plants of northern Kansas, BOT. GAZ. **25**: 255–260. 1898.

The sea blite (*Suaeda diffusa* Wats.) is occasionally found in similar habitats, though usually the clay is dry and loose. It may represent a distinct association of strongly alkaline or saline habitats, or perhaps a primitive growth of alkaline soil.

THE PLAINS RUDERAL ASSOCIATION

Open waste formation.—POUND and CLEMENTS **13**, p. 412.
Plains ruderal formation.—SHANTZ **17**, p. 182.

The first plants to invade disturbed ground in the area studied are annuals, practically all of the plains region. The more important species are *Argemone intermedia* Sweet, *Euphorbia marginata* Pursh, *Solanum rostratum* Dunal, *Festuca octoflora* Walt., *Lappula occidentalis* (Wats.) Greene, *Plantago Purshii* R. and S., *Ambrosia psilostachya* DC., *Boebera papposa* (Vent.) Rydb., *Helianthus petiolaris* Nutt. *Ambrosia trifida integrifolia* (Muhl.) T. and G. is a very conspicuous ruderal in moist soil.

Toward the mountains, and in all except the driest soils, the sweet clover (*Melilotus alba* Desv.) is becoming very frequent in disturbed situations. In such habitats, as in the eastern part of the prairie, it is apparently more successful than native ruderals. The Russian thistle (*Salsola Tragus* L.) behaves as if it were a successful native ruderal, having become thoroughly established.

THE PRIMITIVE BUNCH-GRASS ASSOCIATION

Calamovilfa longifolia consocies.—SHANTZ **17**, p. 46.
Sporobolus cryptandrus (growth).—SHANTZ **17**, p. 46.

Certain of the grasses of the prairie region are very abundant in new growths or in open or sterile situations, as contrasted with other grasses which are found only in more permanent, closed associations, or in mesophytic stations or in soils of considerable humus content. Among these xerophytic grasses distinctive in primitive growths are *Elymus canadensis* L., *Eriocoma cuspidata* Nutt., *Calamovilfa longifolia* (Hook.) Hack., *Sporobolus cryptandrus* (Torr.) Gray, and *Panicum virgatum* L. *Stipa Vaseyi* Scribn., though infrequent in the immediate area, occupies many similar situations throughout the Colorado mountain-front. All of these can grow

in coarse soil, being deep-rooted; some of them build temporary dunes on the sand-hills and on the shores of the Great Lakes. Each species occurs in places alone, but mixed growths of several of these grasses, are about as frequent, and since they are very similar in growth-form, in physiology, and in distribution, they are for the present considered as members of one variable association.

Within the region these growths occur in scattered patches in disturbed situations, frequently in railroad rights-of-way, and usually in loose or sandy soil. Extremely local growths are found on the higher mesas and foothill slopes.

FIG. 9.—*Gutierrezia-Artemisia* growth of a mesa four miles east of Boulder: this end of the mesa differs from the rest of it in that it is not at present pastured, and in that *Gutierrezia* is scarce; *Eriogonum effusum* is conspicuous, though not so in the photograph; September 1912.

THE GUTIERREZIA-ARTEMISIA ASSOCIATION

Gutierrezia-Artemisia association.—SHANTZ **18**, p. 60.
Undershrub formation.—POUND and CLEMENTS **13**, p. 371, in part.
Artemisia frigida society.—SHANTZ **17**, p. 37.
Gutierrezia Sarothrae society.—SHANTZ **17**, p. 37.
Gutierrezia formation.—WATSON **20**, p. 202.

The *Gutierrezia-Artemisia* association, described by SHANTZ (**18**), is typically developed in the plains areas of the region studied. *Gutierrezia Sarothrae* (Pursh) B. and R. is more abundant in the

southern part of the plains region, and is not common in the foothills or even in the mesa-terrace. *Artemisia frigida* Willd. ranges far to the north, and forms an important primitive growth in the mountains to as high as 10,000 feet. The *Artemisia frigida* consocies, therefore, is the important growth of the mountain-front, being quite frequent on talus slopes and gravel slides of the foothills. *Bouteloua hirsuta* Lag. is often associated with *Artemisia;* this growth may represent a separate association.

The *Gutierrezia-Artemisia* growth in the plains of the region contains *Eriogonum effusum* Nutt. and *Grindelia squarrosa* (Pursh) Dunal, sometimes abundantly. There are indications that relative abundance of *Gutierrezia* and *Artemisia* is materially influenced by grazing animals, *Gutierrezia* being apparently more resistant.

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A STUDY OF SYMPHYOGYNA ASPERA

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 196

FLORENCE A. MCCORMICK

(WITH PLATES XXX–XXXII)

The species of *Symphyogyna* are tropical and semitropical liverworts. They grow best in abundant moisture, and especially well in dripping water, but do not thrive in standing water. As a genus distinct from the other genera of Hepaticae, it was first described by NEES AB ESENBECK and MONTAGNE (9) in 1836, and four species were described: *S. brasiliensis*, *S. Hockstettii*, *S. difformis*, and *S. circinata*. Up to this time the first three species had been included in *Jungermanni*. The fourth species was evidently a new one. Additional forms were discovered, and later GOTTSCHE, LINDENBERG, and NEES AB ESENBECK (18) listed 24 species. SCHIFFNER (31), in his census of 1909, reports 27 species.

Symphyogyna is closely related to *Pallavicinia*, which is well known in our flora. These two genera have an interesting parallel series of plant bodies, ranging from the entire ribbon-like form to the deeply dissected and leaflike thallus which closely resembles a fern. While many of the species of *Symphyogyna* are distinctly anacrogynous in form, others with their leaflike lobes are strikingly like the acrogynous Jungermanniales, so that the genus as a whole holds a high rank among the Jungermanniales. Moreover, in the development of the sporophyte and the late differentiation of its sporogenous tissue, it almost approaches the condition of the mosses. STEPHANI (33) considers *Treubia insignis*, with its acrogynous characters, more closely related to *Symphyogyna* than to any other genus, and SCHIFFNER (31) places *Monoclea*, whose position among Jungermanniales has been severely contested by others, especially JOHNSON (22), close to *Symphyogyna*. These two relationships, whether real or imaginary, give some indication of the range of habit of the genus.

Comparatively little is known of the morphology of *Symphyogyna*. LEITGEB (26) gives a general survey of the genus and

emphasizes in particular *S. sinuata*, *S. subsimplex*, and *S. rhizoloba*. He discusses the thallus, including the central strands of smaller cells, the apical cell, and the branches on the ventral side of the thallus. He passes over briefly the sex organs, giving no figures of the antheridia and few of the archegonia. He illustrates a close series of stages of the young sporophyte, but states that the later details in the development of the sporogenous tissue into spore mother cells and elaters remained dark to him. The only observations which he makes concerning the older sporophyte are that the apex of the sporophyte undergoes secondary divisions, to which is due the beaklike form of the tip of the capsule; that the differentiation into elaters and mother cells occurs relatively late; that the former are arranged in a direction parallel to the embryo axis and that they are uniformly distributed throughout the capsule. TANSLEY and CHICK (34) discuss more fully the structure of the central strand of the thallus. No other papers bearing directly on the morphology of the genus have been published, and only occasional references in connection with other liverworts have been made.

The highly developed conducting tissue of the gametophyte and the mosslike development of the sporophyte make the genus peculiarly interesting. It was hoped that a complete life history of the species might be secured, but many stages are lacking. While little is added to LEITGEB's account, a few facts concerning a genus about which so little is known may be of interest.

Material

The material was collected in the vicinity of Xalapa and Texolo, Mexico, by Dr. W. J. G. LAND and Dr. CHARLES R. BARNES in the autumns of 1906 and 1908, and by Dr. LAND in the autumn of 1910. It was killed in the field in 6 per cent formalin made up with 50 per cent alcohol. Excepting for the young embryos, this killing agent was found to be satisfactory, and in fact it is almost a necessary one when time and light baggage are to be considered. From the alcohol-formalin solution the material was transferred to 50 per cent alcohol, and the process of dehydration was carried on through series of absolute alcohol and xylol

into pure xylol, was imbedded in paraffin and cut, usually, 5 μ thick. Safranin and gentian violet, safranin and lichtgrün, and Haidenhain's iron-alum hematoxylin were the stains used.

Thallus

Symphyogyna aspera (figs. 1 and 2) has a rhizome-like portion which closely adheres to the soil, and from this rhizome arise somewhat inclined aerial branches. GOEBEL (**15**), in his description of *S. sinuata*, states that the winged shoots can again decrease at the apex and become stolons, but usually they conclude their growth after reaching a definite medium size, and then at their base they form a ventral lateral shoot which continues the growth as a stolon, subsequently rises above the substratum, broadens out, again forms a dorsiventral shoot, and so on. His illustration of *S. sinuata* shows a chain of five such generations. In *S. aspera* no indications were noted that the apex of the thallus may act as a stolon, but growth by a basal stolon is characteristic of this species also.

Rhizoids are very abundant, forming thick mats upon the ventral surface of the rhizome and parts of the aerial branches in contact with the soil. As has been previously noted, especially by BOLLETER (**2**) in *Fegatella conica* and by CLAPP (**7**) in *Aneura pinguis*, the ends of the rhizoids are curiously branched, twisted, and often greatly enlarged (figs. 3 and 4). The branched ends often tightly surround particles of foreign material. If there are cross-walls near the ends of the rhizoids they must be quite rare, for none were observed in the material examined.

Fungi are abundant, especially in the rhizoids (figs. 5 and 6). A favorable view gave indications that the fungus had penetrated the tip of the rhizoid (fig. 6). The fungous species could not be determined from the preserved material, but evidently more than one species is present. Some hyphae are large and abundantly septate (fig. 5), and other hyphae are quite small, so that the septations, if present, could not be distinguished. Fungi have been frequently reported among liverworts, especially by LEITGEB (**26**), KNY and BOTTGER (**24**), J. PEKLO (**30**), GOLENKIN (**16**), NĚMEC (**28** and **29**), CAVERS (**5**), JANSE (**21**), GARJEANNE (**13** and **14**),

and CLAPP (**7**). GARJEANNE has done an extensive piece of work in having examined over 30 species, and he concludes that the fungi neither do harm nor good to the host plant.

In transverse section, the rhizome of *S. aspera* is somewhat irregularly oblong (fig. 7). The cells are undifferentiated except in the central region, where there is a group of small, thick-walled cells which stand out in sharp contrast with the much larger, thinner-walled cells surrounding them. In longitudinal section they appear as very narrow, greatly elongated cells, whose pointed ends dovetail into each other (fig. 8). LEITGEB (**26**, p. 69) gives the length of the cells in *S. sinuata* as 0.3 mm. and the breadth 0.009 mm. In *S. aspera* the cells are 0.537 mm. long and 0.008 mm. in diameter.

The aerial part of the thallus has the same general structure as the rhizome (fig. 9). There is a central region of small, thick-walled cells surrounded by broader, thin-walled cells, which together form the midrib of the thallus. From the midrib the thallus narrows abruptly into winglike extensions consisting of one layer of cells. By treating the thallus, either the rhizome or aerial parts, with Schulze's macerating solution, the cells of the central area can be separated entire, and by staining them with Delafield's hematoxylin, the structure of the cell walls may be seen distinctly (fig. 10). This treatment enables one to get a more accurate measurement of their length, and it is also interesting to know that they remain intact after the action of this reagent. The cells of the wing are disintegrated, but some cells surrounding the central strand may remain intact provided the action of the reagent is not too long (fig. 8). These long, narrow cells, with their thick walls and spirally arranged pores, make *Pallavicinia*, *Hymenophyton*, and *Symphyogyna* peculiarly interesting. They were discovered by Sir WILLIAM HOOKER in 1816 in *Pallavicinia Lyellii*. In 1864 GOTTSCHE (**17**) described them in *S. sinuata*. LEITGEB (**26**, p. 69) describes the cells with their spirally arranged pores, but he has no illustrations. FARMER (**10**) adds little to LEITGEB'S account, though he gives a good drawing of the transverse section of the rhizome, and also one showing the lack of continuity between the strand of the main part of the thallus and that of the ventral branch. TANSLEY and CHICK (**34**) discuss fully the

strands in *Pallavicinia*, *Hymenophyton*, and *Symphyogyna*, and they have demonstrated with eosin that in *Pallavicinia Lyellii* the strands conduct water. Their detailed drawing of part of a cell showing pores (*pl. 1. fig. 4*) is representative of the pores in *Symphyogyna*, with the probable exception that in *S. aspera* the pores are more regularly arranged and more obliquely spiral. Sections of the thallus treated with acidulated alcohol and stained with methylene blue, following Mayer's method given by HAAS and HILL (19), gave the test for pectose by showing the middle lamella stained a deeper blue (fig. 11). The pores are so narrow that except in very thin sections they are readily overlooked in transverse sections.

In the species of *Symphyogyna* which he examined, LEITGEB found the dolabrate apical cell like that in *Pallavicinia*, etc., though for *S. sinuata* he makes the statement that at first glance one might think the apical cell like that in *Pellia calycina*, *Blasia*, etc., which is the well known wedge-shaped cell. However, he considers that such a view is an erroneous one, and that the apical cells of all the species of *Symphyogyna* are alike. *S. aspera* has two types of apical cell, the dolabrate and the wedge. STEPHANI identified the species and grateful acknowledgments are due him. However, in the material sent to him, the part collected at Texolo, Mexico has the wedge-shaped apical cell, and that collected at Xalapa has the dolabrate apical cell. Moreover, the thallus of the material collected at Texolo is slightly broader and less deeply lobed than the material collected at Xalapa. The last two characters may be overlooked as due to a difference in environment; but when to them is added a difference in the apical cell, one may be justified in considering the material as representing different species, especially since species are often separated for less convincing reasons. If both forms belong to the same species, then there is the interesting situation of two types of apical cell in mature plants of the same species (figs. 12–16). However, CAMPBELL (3) reports two types of apical cell in *Calycularia radiculosa*.

In the dolabrate cell a segment is cut off alternately to the right and left. The primary segments on both sides are divided longitudinally, and from the middle secondary segment in each side can be traced the one-layered winglike extensions of the thallus (fig. 17).

From the nature of the dolabrate apical cell there cannot be true dichotomy, if by the term "true dichotomy" is meant the division of the apical cell into two segments alike in shape and size and also like the original apical cell. This seems to be the only standard for the determination of true dichotomy; but frequently the organization of the apical cell of the branch occurs so close to the apical cell of the main branch that the mature thallus has the appearance of true dichotomy. In the liverworts which have a wedge-shaped apical cell true dichotomy is the probable form of branching; for a cell of this form can be divided into two cells which are alike in size and shape and also like the parent cell; although it is possible that segments near the apical cell may organize a new apical cell.

Two-celled mucilage hairs are organized from segments close to the apical cell, and these occur on both the dorsal and the ventral sides. These mucilage hairs at first project over the apical region of the thallus; but as the thallus grows new ones are formed and the older ones, apparently in good condition, can be seen far back from the apex. LEITGEB (**26**, p. 73) states that they are more abundant on the ventral than on the dorsal side of the thallus, and this statement seems to be true also for *S. aspera*. The mucilage hairs are formed only in the immediate vicinity of the apex.

Branching on the ventral side of the thallus of *S. aspera* is quite common. LEITGEB discusses rather extensively the situation, and traces the branches close to the apical cell.

Sex organs

Symphyogyna is dioicous, the plants bearing antheridia usually being more slender than those bearing archegonia.

ARCHEGONIA

The archegonia are borne in groups in the dorsal side of the thallus. Each group is surrounded by a deeply dissected involucre, which is attached on one side to the thallus. Usually there is a group at the place of forking of the thallus, but they are not restricted to that region, and often there are several groups close together on one branch. The archegonia have their origin close

to the apical cell (fig. 18), and in this particular thallus the initial shown is the only one of the group which had made its appearance. Moreover, a cell which would have been actively involved in the development of the involucre is in the second row to the left of the initial. Since similarly shaped cells may be distinguished in several sections, it seems probable that the involucre has its origin from a row of meristematic cells. As the archegonia (figs. 19–25) develop, the thallus below them becomes meristematic, so that the archegonia come to be arranged on a pad, as is common among the anacrogynous Jungermanniales.

The earliest stage of an archegonium might readily be mistaken for a young mucilage hair; but a mucilage hair may be distinguished by the bend which it makes very early toward the apical cell. By transverse divisions the archegonial initial is divided into a tier of three cells, and the outermost cell by three longitudinal walls is divided, in the usual way, into four cells, an inner cell surrounded by three outer cells (fig. 21). The neck of the archegonium is long, and the neck cells are spirally arranged, as in the mosses (fig. 6). There were counted 13 neck canal cells in one archegonium, and in another archegonium the neck canal row was in part double (fig. 28). The egg is small, and in that respect it resembles the egg of mosses. An undoubted case of fertilization was not seen, though fig. 27 represents an archegonium which may be interpreted as showing fertilization. The withered neck cells and the presence of young embryos in the same cluster add weight to this interpretation.

ANTHERIDIA

The antheridia are grouped in compact masses on the midrib on the dorsal side of the thallus, and each antheridium is surrounded by a small involucre somewhat similar to the one which surrounds each group of archegonia. (SPRUCE **32**, *pl. 30*), in a diagrammatic way, illustrates the antheridial scales of *S. trivittata*. More than one group of antheridia may occur on the same thallus, indicating a cessation followed by a renewal of activity in the production of antheridia. This feature LEITGEB observed in the species which he investigated (**26**, p. 74). No plants bearing antheridia were found in the material which gave the young stages

of archegonia, and though many antheridial plants were mixed with the plants bearing sporophytes, the antheridia with few exceptions had discharged their sperms and fallen off. The few antheridia that were found seem to have been delayed ones. No very young stages were obtained, but the older ones indicate the method of development usual in the Jungermanniales (figs. 29–31). The body of the antheridium is nearly spherical, and the stalk is short and slender.

Sporophyte

The fertilized egg is divided into two cells by a transverse wall (fig. 32), and a third cell is cut off by a wall parallel to the first. In the material studied karyokinetic figures were entirely lacking in the young embryos, so that it is impossible to state with certainty whether it is the epibasal or hypobasal cell that divides. LEITGEB mentions that in *S. rhizoloba* it is the inner cell which remains undivided, and that this cell can be recognized in well developed embryos. He gives a close series of stages for this species, and apparently after the row of three cells is formed there is some variation in the subsequent walls. However, he states that the outermost cell is divided by an oblique wall. This may also be true for *S. aspera* (fig. 33). This oblique wall is the beginning of the apical growth which LEITGEB emphasizes very strongly for *S. rhizoloba*, and in fact later stages of *S. aspera* (figs. 35–37), with their marked segmentation, seem to verify this method of development.

The young embryo is slender, and it is early shown that the uppermost part is the region most actively involved in cell division, and that part is also marked by a denser cell contents. The middle part is concerned with elongation, and there the cells lengthen, with little activity in cell division (fig. 37). The cell contents in this part is less dense than in the upper part, and it is also greatly vacuolate. The innermost cell of the embryo may very early divide, as shown in fig. 34, but, judging from the general contour of the young embryos and without the aid of figures, it seems probable that cell multiplication in this part of the embryo is restricted to very few divisions. Periclinal walls are formed

separating the amphithecium from the endothecium. Three wall layers are formed, the middle layer being apparently cut off from the outer layer (fig. 38). The walls of the outermost layer of cells thicken as the sporophyte matures, and the two inner layers do not entirely disappear, so that the mature capsule wall is not one layer thick, as has been reported for some species of *Symphyogyna* (1). Plastids are quite numerous in the cells of the capsule wall. The beaklike extension of the apex of the capsule is prominent, as LEITGEB noted in the species which he studied (fig. 38). The foot of the mature embryo is often somewhat anchor-shaped, but more frequently there is a gradual narrowing toward the tip of the foot, which is always bent over in a mosslike manner (fig. 39). The cells of the thallus surrounding the sporophyte become greatly disintegrated, and the foot of the mature sporophyte is imbedded in a mucilaginous mass. The pad upon which the archegonia stand elongates as the embryo grows, and the non-functioning archegonia are carried up to the apex of the calyptra. Five young embryos were found in one group, and it is quite common to find two or three together. The potentially sporogenous cells are sharply delimited from the beginning by their denser cell contents, larger nuclei, and active cell division.

SPORE MOTHER CELLS

The subsequent history of the sporogenous part of the embryo is interesting and important, for there must be a fundamental process which lies back of the formation of the curiously lobed spore mother cell so uniformly characteristic of the Jungermanniales. In the Marchiantiales it is a simple matter to dismiss the formation of the spore mother cells with the familiar expression that they "round up"; but the formation of a lobed mother cell demands more consideration. However, the stages immediately preceding the rounding up of the mother cells in the one group, and the lobing of the mother cells in the other group, are fundamentally the same. These stages in permanent mounts show the sporogenous cells irregular in shape, and bearing every indication that they were plasmolyzed in the fixation or imbedding. As mentioned above, LEITGEB frankly admits that he did not understand the processes

leading up to the formation of the spore mother cells and elaters; and KIENITZ-GERLOFF (23), in discussing the Jungermanniales, adds nothing of importance. While a great deal has been written on the mitoses in the spore mother cell, literature on the formation of the mother cell is strikingly scanty. LECLERC DU SABLON (25) has made some important observations. He carefully investigated the development of the sporophyte of *Frullania dilata*, and with that species he compared *Scapania compacta*, *Pellia epiphylla*, *Aneura pinguis*, *Targionia hypophylla*, and *Sphaerocarpus terrestris*. He emphasizes some important points, namely, that there is an early differentiation between elaters and spore-producing tissue; that the elater is the equivalent of a row of mother cells; and that the walls between spore mother cells and elaters early become gelatinized. In the following statement he considers the irregularity of the potential spore mother cells, but does not seem to consider this feature of any importance.

> Tandis que certaines masses protoplasmic (*s*) destinées à devenir cellules-mères de spores s'accroissent régulièrement sur tout leur pourtour et présentent l'aspect d'amibes à peu près isodiamétriques d'autres (*el*) s'allongent exclusivement dans une direction, et acquièrent la forme se produit cet accroissment rapide, si c'est par formation de cellules nouvelles, ou par l'elongation des cellules déjà existantes.

Again he says (25, p. 169):

> Les cellules-mères continent a s'accroitre pendant longtemps encore, puis on voit apparaître à leur surface de petits sillons, premier indice d'une division en quatre spores. Pendant que ces sillons se creusent et accusent ainsi de plus en plus la forme de tétrade que prend la cellule, le noyau se divise en quatre, puis le protoplasma se divise de même, et à partir de ce moment on peut dire que la division de la cellule-mère en quatre spores est consommée, les phénomènes qu'on observe ensuite étant d'un ordre tout a fait accessoire.

CAMPBELL (4, p. 111) does not agree with LECLERC DU SABLON'S observations on the disappearance of the walls in the sporogenous tissue, and in this connection he makes the following statement:

> A great many carefully stained microtome sections of a large number of liverworts belonging to all the principal groups have been examined by me and invariably the presence of a definite cell wall could be demonstrated at all stages.

Again, he says (**4**, p. 34) in regard to the Ricciaceae:

As the sporogonium increases in diameter, the central cells begin to separate and round off. Their walls become partially mucilaginous and in microtome sections stain strongly with Bismarck-brown or other reagents that stain mucilaginous membranes. With this disintegration of the division walls the cells separate more and more until they lie free within the cavity of the sporogonium.

FARMER (**10**), in discussing *Pellia epiphylla*, says in regard to the spore mother cell:

At first more or less irregularly spherical, it soon becomes four-lobed, and these lobes increase in size, chiefly owing to radial extension, so that the spore mother cell ultimately comes to consist of four large sacs whose cavities communicate with each other by means of a small central space common to them all.

In a later paper (**11**), in summing up the characteristics of the sporogenous tissue of the Hepaticae, he says:

A third feature of some interest, and which in practice is especially noticeable, is that just at the period of the spore-formation it becomes exceedingly difficult to fix the cells without some contraction. This is the more remarkable since the nuclei, which may happen to be dividing in either earlier or later stages, present not the slightest difficulty. Moreover, the cytoplasm also stains deeply with most nuclear stains, and everything points to the conclusion that there is something going on in the cell during this so-called reduction division which is not met with at any other period, whether in resting or dividing cells.

WILSON (**34**), in regard to *Mnium hornum*, says:

FARMER has already noted that at the reduction division the spore mother cells of the Hepaticae can only be fixed with great difficulty. This is especially the case in the Muscineae.

Of the spore mother cell of *Pallavicinia decipiens*, FARMER (**10**) says:

The mother cell becomes tetrahedrally lobed, and the cell walls at their inner angles grow into the cell cavity towards the nucleus.

These citations are representative of the literature on spore-formation in the Hepaticae.

While the spore mother cells of *Symphyogyna* are comparatively small, the large amount of sporogenous tissue in each sporophyte and the deep lobing of the mother cells make it a favorable species

for study. A young sporophyte, such as is represented in part by fig. 40, shows no differentiation in the sporogenous tissue, though some of the longer cells may be considered as potential elaters. In an older sporophyte (fig. 41) the elaters by their elongation are in sharp contrast with the cells which will produce spore mother cells. In such a sporophyte the protoplasts have contracted slightly from the cell walls, which are still distinctly seen, and the intervening spaces are filled with a mucilaginous substance which stains a faint yellow in gold orange. The protoplasts show no difference in their staining, and excepting the difference in shape are alike in general structure. In older sporophytes (fig. 42) the elaters have assumed their characteristic shape, and their protoplasts are undergoing the peculiar changes incident to the formation of the spiral thickenings. The walls between the cells are still distinct, but they have lost some of their sharpness, and the mucilaginous substance stands out more distinctly when stained with gold orange. The pronounced irregularity of the shape of the cells which are to produce spore mother cells is a striking feature, and this irregularity continues until the lobed mother cell is fully mature. From the beginning of the differentiation of elater-producing cells and sporogenous cells (fig. 43), the division of the sporogenous cells continues, and frequently lobed mother cells and sporogenous cells still in division are seen in the same capsule.

Since living material of *Symphyogyna* could not be obtained to verify the observations made from prepared slides, *Pellia epiphylla*, *Aneura pinguis*, *Pallavicinia Lyellii*, *Cephalozia bicuspidata*, and *Porella platyphylla* were studied. The sporogenous tissue was separated from the walls of the sporophyte and mounted in water, and also other material was studied in the crushed sporogonium without the addition of any reagent whatever. The living cells were immediately examined under the microscope, and they were found to show the same irregular amoeboid forms which had been noted in the permanent mounts. Sporophytes from the same material were killed in different strengths of chromo-acetic, with and without osmic acid, and in Benda's solution, and in each case the results showed the same irregularity of the sporogenous cells (figs. 56–60). Moreover, in the laboratory all slides

of sporophytes of liverworts belonging to the Marchantiales, Jungermanniales, and Anthocerotales, in the stages preceding the maturity of the spore mother cell, show the same situation. These slides are the accumulation of years and have been made by different people. On account of the lobing of the mother cell, the Jungermanniales show the irregularity to a more marked degree and for a longer time, but before the rounding up of the mother cell in the other groups, similar irregularity in shape and peculiarity in staining may be seen. From the observations made, it may be a reasonable interpretation that during the development of the tissue which eventually gives rise to spore mother cells, the protoplasts assume amoeboid forms, and the walls undergo a change. Older stages of the sporophyte (figs. 42–44) show increase in the accumulation of the mucilaginous substance and also the reducing of the cell walls into a substance of that nature. HOFMEISTER (**20**, p. 81) notes that the walls become considerably thicker, and that the substance of these walls is converted into a substance which swells extensively in water. There are striations which readily could be mistaken for walls, but any mucilaginous substance may give that effect.

Development of the spore mother cells in an individual sporophyte is not simultaneous, as may be seen in fig. 44, which shows the beginning of the lobing of one mother cell and other sporogenous cells still dividing. As the mother cell begins to become lobed, the extensions of the protoplast become more marked and vacuoles seem to play an important part in the process of lobing. A characteristic stage (fig. 45) shows the orientation of the four lobes and in each lobe there is a large vacuole. Later (figs. 46 and 47) the large vacuoles are broken up into smaller ones and the cytoplasm is uniformly distributed throughout each lobe. Apparently the nucleus always occupies the central position of the mother cell.

DAVIS (**8**), in discussing the spore mother cell of *Anthoceros*, asks the question whether the cytoplasm could be intrusted with so important a task as the preparation of a chloroplast for each of the four nuclei. A similar question may be asked in regard to the lobing of the mother cells. In the lobing of the mother cells it seems as if there are two alternatives: either the nucleus, long before it

shows any visible signs of activity, affects the cytoplasm to such a degree that the four lobes are organized in advance of the reduction division of the nucleus; or the cytoplasm, in addition to the nucleus, is an important factor in the reduction division.

The quadripolar spindle may be distinctly seen at the beginning of the reduction division (fig. 51); but the later stages (figs. 52 and 53) verify MOORE'S interpretation (27) rather than the interpretation of FARMER (10). The chromosomes are very short and thick (fig. 48).

The four young spores gradually separate (fig. 51). At this stage of the sporophyte the greatly elongated nuclei of the elaters, with their strong bands of chromatin and prominent nucleoli, are very striking. The mature spore (fig. 55) measures about 18.3 μ in diameter. The echinations are short but very sharp, and a surface view (fig. 53) shows them distinctly reticulate. Spores with two nuclei (fig. 54) are not very common, but enough were found to lead one to think that there is a feeble tendency toward intrasporal germination. The mature elaters (fig. 55) have two very prominent spirals.

Summary

1. The thallus of *Symphyogyna aspera* has a central strand of greatly elongated cells which taper at both ends. The walls of these cells have narrow pores which are spirally arranged.

2. Like the other species of the genus, *S. aspera* is dioicous. The plants bearing antheridia are more slender and less freely branched than the plants bearing archegonia.

3. The antheridia are scattered over the thickened part of the thallus on the dorsal side. Each antheridium is surrounded by a scale.

4. The archegonia are in groups on the dorsal side of the thallus. Each group is on a padlike extension of the thallus and is surrounded by an involucre.

5. More than one embryo may be formed in a group, but so far only one has been found to reach maturity.

6. As the embryo elongates, the calyptra and pad also elongate and the old archegonia are left in the tip of the calyptra.

7. The young embryo develops by segmentation similar to that formed by a dolabrate apical cell.

8. The sporogenous tissue is differentiated relatively late in the history of the sporophyte.

9. The cells which are to form elaters may early be distinguished from the cells which are ultimately to give rise to the spore mother cells. The former cells elongate without further division, while the latter cells undergo several divisions.

10. The walls of the sporogenous mass of cells become gelatinized, and the protoplasts are potentially free in the gelatinous substance.

11. The spore mother cells attain their lobing by a slow amoeboid change of the protoplast, and in this movement vacuoles seem to play an important part. The examination of the living sporogenous tissue of other Jungermanniales verifies the occurrence of this phase in them also.

12. Spores with two nuclei have been found, though this is not a usual condition.

Grateful acknowledgments are due Professor JOHN M. COULTER for advice and criticism, and to Dr. W. J. G. LAND, who supplied all the material and to whose help and encouragement the completion of the paper is due.

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EXPLANATION OF PLATES XXX–XXXII

Symphyogyna aspera

FIG. 1.—Thallus with antheridia; ×2.

FIG. 2.—Thallus with sporophytes; ×2.

FIGS. 3, 4.—Ends of rhizoids; ×700.

FIG. 5.—Rhizoid containing a septate fungus; ×700.

FIG. 6.—Tip of rhizoid showing a fungus; ×1600.

FIG. 7.—Transverse section of rhizome; ×70.

FIG. 8.—Outline of a longitudinal view of a cell from the central region and three adjoining cells; ×180.

FIGS. 9, 10.—Cells of thallus adjoining cells of central region; ×180.

FIG. 11.—Transverse section of aerial part of thallus; ×170.

FIG. 12.—Part of cell of central region showing pores; ×2300.

FIG. 13.—Transverse section of cells of central region; ×1300.

FIG. 14.—End view of apical cell; ×645.

FIG. 15.—Section of apical cell parallel with the surface of the thallus; ×645.

FIG. 16.—Median longitudinal section of apical cell; ×645.

FIG. 17.—Median longitudinal section of wedge-shaped apical cell; ×645.

FIG. 18.—Transverse section of wedge-shaped apical cell; ×645.

FIG. 19.—End view of apical cell showing segment from which the wing has its origin; ×645.

FIGS. 20–22.—Stages in the development of the antheridium; ×700.

FIG. 23.—Median longitudinal section of thallus showing apical cell, initial of archegonium, beginning of involucre, and beginning of development of central cells; ×645.

FIGS. 24–30.—Stages in the development of the archegonium; ×645.

FIG. 31.—Archegonium showing spiral arrangement of neck cells; ×140.

FIG. 32.—Archegonium showing probable fertilization; ×1300.

FIG. 33.—Archegonium showing a doubling of the neck canal cells in one part; ×645.

FIGS. 34–38.—Stages in the development of the embryo; ×645.

FIG. 39.—Older stage of embryo; ×450.

FIG. 40.—Another view of the basal part of the embryo shown in fig. 39; ×450.

FIG. 41.—Tip of mature sporophyte; ×180.

FIG. 42.—Foot of mature sporophyte; ×180.

FIG. 43.—Part of young embryo showing sporogenous tissue and walls, and length of sporogenous tissue; ×860.

FIG. 44.—Part of sporogenous tissue showing the beginning of contraction of protoplasts; ×860.

FIGS. 45–47.—Stages in development of sporogenous tissue; ×860.

FIG. 48.—Early stage of lobing of mother cell; ×1600.

FIG. 49.—Late stage of lobing of mother cell; ×1600.

FIG. 50.—Mature spore mother cell; ×1600.

FIG. 51.—Mature spore mother cell just before reduction division; ×1600.

FIG. 52.—Spore mother cell during reduction division; ×1600.

FIG. 53.—Homotypic division of spore mother cell; ×1600.

FIG. 54.—Young spores nearly separated; ×1600.

FIG. 55.—Surface view of echinations of spore coat; ×1600.

FIG. 56.—Mature spore; ×1600.

FIG. 57.—Mature spore with two nuclei; ×1600.

FIG. 58.—Mature elater; ×1600.

Pellia epiphylla

FIG. 59.—Outline of spore mother cell from living material; ×1300.

Aneura pinguis

FIGS. 60–64.—Outlines of sporogenous cells from living material; ×1300.

FIGS. 65–67.—Outlines of sporogenous cells from preserved material; ×1600.

Pallavicinia Lyellii

FIGS. 68–75.—Outlines of sporogenous cells from living material; ×1300.

FIGS. 76–83.—Outlines of sporogenous cells from preserved material; ×1600.

Cephalozia bicuspidata

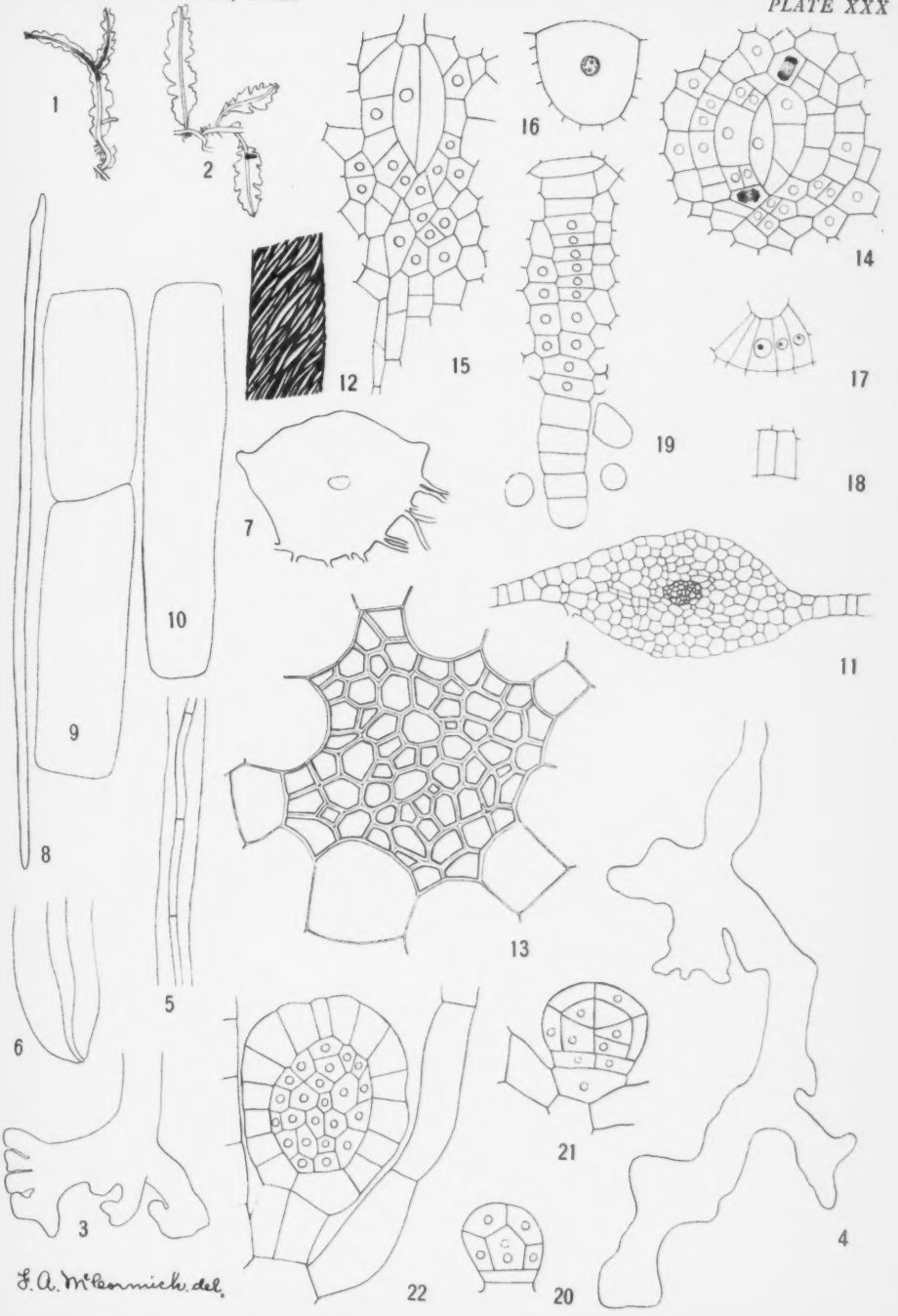
FIGS. 84–87.—Outlines of spore mother cells from living material; ×1300.

FIGS. 88–93.—Outlines of spore mother cells from preserved material; ×1600.

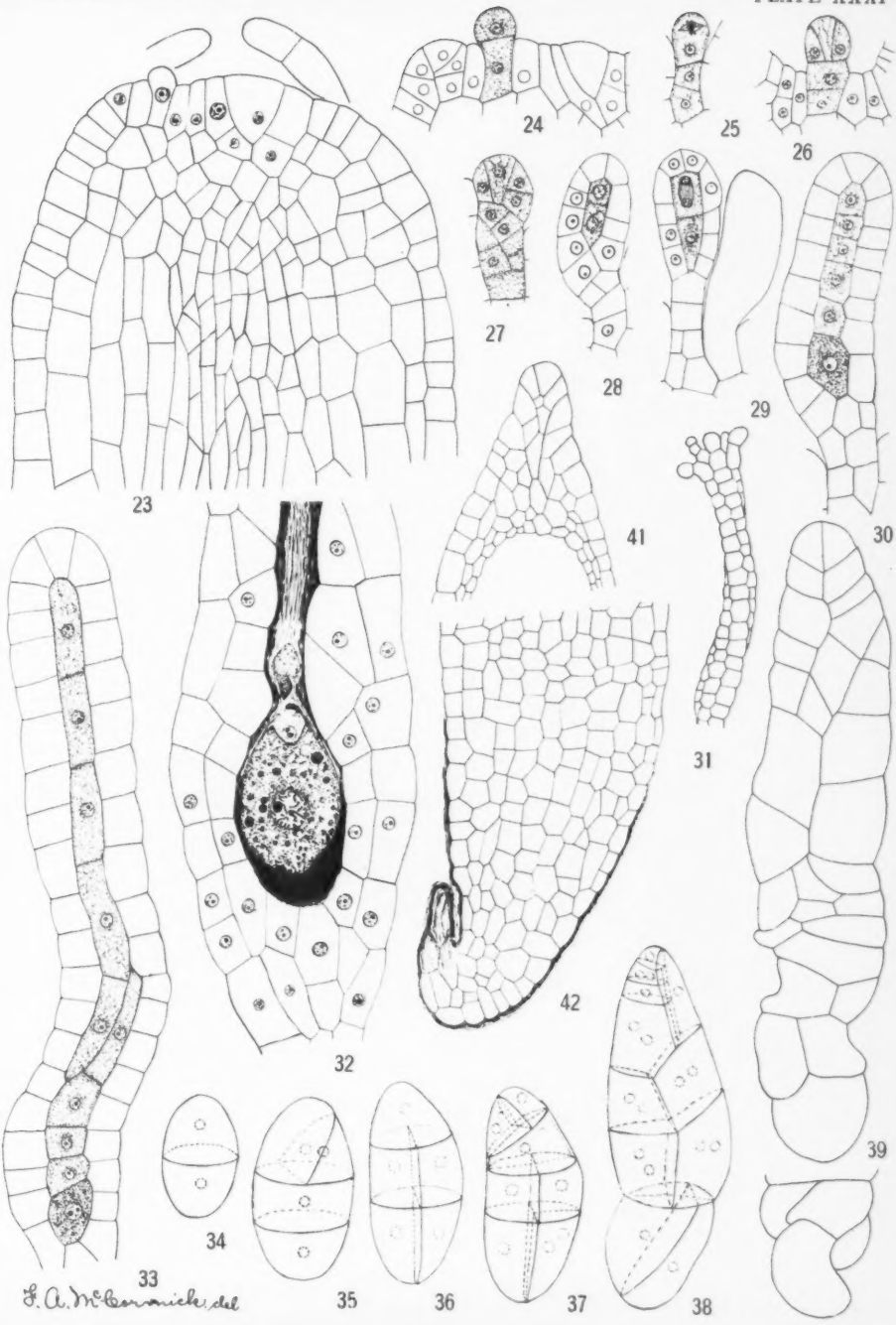
Porella platyphylla

FIGS. 94–99.—Outlines of spore mother cells from living material; ×1300.

FIGS. 100–102.—Outlines of spore mother cells from preserved material; ×1600.



McCORMICK on SYMPHYOGYNA



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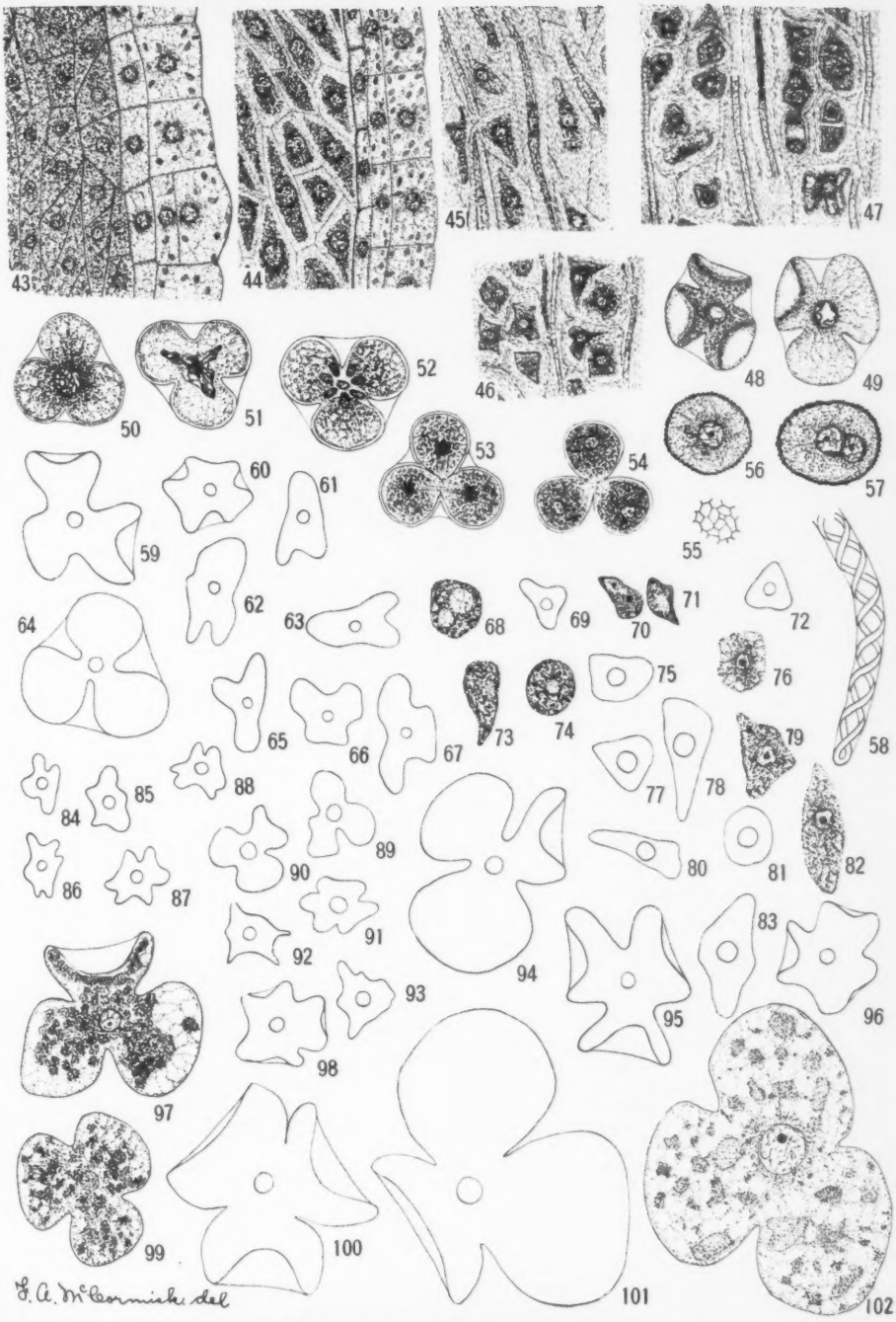

McCORMICK on SYMPHYOGYNA

SPERMATOGENESIS IN MARSILIA

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 197

LESTER W. SHARP

(WITH PLATES XXXIII AND XXXIV)

Introduction

In 1912 the writer (**6**) published the results of an investigation of spermatogenesis in *Equisetum*. The principal conclusion was that the blepharoplasts of bryophytes, pteridophytes, and gymnosperms are derived ontogenetically or phylogenetically from centrosomes. The basis for this conclusion was found in the behavior of true centrosomes and cilia-bearing organs in plants and certain animals, special emphasis being laid upon the remarkable centrosome-like activity of the blepharoplast of *Equisetum*.

The behavior of the blepharoplast of *Marsilia*, as described by SHAW (**7**) and by BELAJEFF (**3**) in 1898 and 1899, was also used as a strong argument for the centrosome nature of the blepharoplast. Since these accounts show incompleteness and uncertainty with regard to several points, and since the two writers reached contrary theoretical conclusions, it was deemed advisable to examine certain material[1] at hand with a view toward establishing the true state of affairs in *Marsilia*.

An extensive historical résumé of researches on centrosomes and cilia-bearing structures in plants was presented in the writer's paper on *Equisetum* and will not be repeated here. To the list of papers given should be added those of ALLEN (**1**) and WALKER (**8**) on *Polytrichum*. In the present work only those dealing with *Marsilia* need to be reviewed.

The early papers of CAMPBELL (**4, 5**) on *M. aegyptiaca* and *M. vestita* show the general topography of the male gametophyte. The sequence of wall-formation was not determined in the former species, and great irregularity was reported in the latter. CAMPBELL made out none of the cytological details of spermatogenesis.

[1] The writer is indebted to Dr. C. J. CHAMBERLAIN for a portion of the material used.

In 1898 BELAJEFF (2) described the development of the male prothallium in several Hydropteridineae. In *Marsilia elata* he worked out carefully the exact sequence of walls, which, it will be seen, resembles rather closely that in *M. quadrifolia* as described below. In the latter species BELAJEFF did not figure a developmental series.

SHAW (7) in the same year gave an account of the blepharoplast in *M. vestita*. According to this investigator, a small granule or "blepharoplastoid" appears near each daughter nucleus at the telophase of the second spermatogenous mitosis. During the prophases of the third mitosis it divides and then degenerates in the cytoplasm, while a blepharoplast appears near each spindle pole at metaphase. In the following cell generation (spermatid mother cell) the blepharoplast divides to two which occupy positions near the spindle poles through the fourth or final mitosis. Each spermatid thus receives a blepharoplast. The latter soon shows a small internal granule which multiplies and forms a band; this elongates in close union with the nucleus and bears the cilia. In these facts SHAW found no grounds for the homology of the blepharoplast and the centrosome.

In the following year BELAJEFF (3) reported the results of his researches on *M. macra* and *M. vestita*. He found centrosomes, which he did not hesitate to call them, at the spindle poles in the last three spermatogenous divisions. With regard to the first division he was uncertain; the figure which he gave as possibly representing the first mitosis almost certainly represents the second. He was inclined to identify the centrosome of the second mitosis with the "blepharoplastoid" of SHAW, but believed it to be continuous from the time of its origin, dividing after each mitosis in preparation for the next, and in the spermatid performing the function of a blepharoplast. BELAJEFF regarded this as a strong confirmation of his previously stated theory that the blepharoplast and the centrosome are homologous structures.

In the present paper an attempt will be made to clear up the points left in doubt by these earlier workers, and to add new details which will make it possible to decide between their divergent views concerning the morphological nature of the blepharoplast.

Material and methods

Sporocarps of *Marsilia quadrifolia* were cut open and placed in water at room temperature. Sori were fixed at short intervals until sperms were seen swimming in large numbers, a period of 10 or 12 hours.

Several fixing reagents were employed, including those of Flemming and Benda. The best results were obtained in preparations stained with Haidenhain's iron alum-hematoxylin after the following fixing fluid: 1 per cent chromic acid 25 cc., water 75 cc., glacial acetic acid 1 cc., 2 per cent osmic acid 14 drops.

Description

THE MALE GAMETOPHYTE

A comparison of figs. 1–7 with fig. 8 will do more than a written description to make clear the development of the male gametophyte.

At the time when the gelatinous ring bearing the sori escapes from the sporocarp, the microspore has in section the appearance shown in fig. 1. The nucleus occupies a central position, and large starch grains lie scattered throughout the cytoplasm. These very soon move to the periphery, leaving the nucleus surrounded by a zone of granular cytoplasm. The nucleus then passes to the side of the spore, usually the side opposite the point where the spore met the others of the tetrad, and cuts off a small prothallial cell (wall 1, figs. 2, 3). No "basal cell," such as BELAJEFF (2) figures above the prothallial cell in *M. quadrifolia*, was found in our material.

The next wall (wall 2, fig. 4) passes through the center of the spore. The two hemispherical cells so formed behave alike, each producing an antheridium in the following manner. A curved wall (wall 3, fig. 5) cuts off a large wall cell. A small sterile cell is next formed in the angle between walls 2 and 3 (wall 4, fig. 6). Wall 5 then cuts off a peripheral cell (fig. 7) which completes the wall of the antheridium and defines the limits of the primary spermatogenous cell. There are no centrosomes in any of these mitoses.

Each primary spermatogenous cell by four successive divisions gives rise to a group of 16 spermatids (figs. 9–12). Since the two spermatogenous masses formed in the two hemispheres are entirely

separated from each other by the sterile cells cut off by the walls numbered 4, it seems reasonable to hold with BELAJEFF that the microspore develops two symmetrically placed antheridia separated by wall 2. The prothallial cell degenerates during the later antheridial divisions.

The foregoing account agrees in its essential features with that given by BELAJEFF (2) for *M. elata*, but in that form the development in the two hemispheres is not so symmetrical. In a very few cases we have seen wall 3 in the upper hemisphere strike the spore wall rather than wall 2, which results in a condition more like that in *M. elata*.

SPERMATOGENESIS

As stated above, each primary spermatogenous cell gives rise, by four successive divisions, to 16 spermatids. In these mitoses the chromosomes behave as in ordinary vegetative mitoses, and in view of the purpose of the present study do not require special description. Attention will therefore be directed wholly to the centrosomes and associated structures.

First spermatogenous mitosis.—The primary spermatogenous cell shows nothing which can be called a centrosome. The cytoplasm is dense and contains many small granules, but it is evident that no significant rôle can be attributed to them. The spindle forms without the agency of any visible kinetic center. At late prophase and metaphase it ends rather indefinitely at the poles (fig. 13), but during anaphase these regions appear denser (fig. 14). A little later long and very distinct radiations develop about each pole; at their focus there is a dense and finely granular appearance (fig. 15), but no distinct body is formed. At telophase these polar achromatic structures disappear; in fig. 16 their last remnants may still be seen.

Second spermatogenous mitosis.—In the prophases the second mitosis is similar to the first. The spindle at first ends indefinitely (fig. 17), but during early anaphase it rapidly becomes pointed. Long radiations develop as in the preceding mitosis, and at each pole a very minute and intensely staining granule appears (fig. 18). This is the centrosome. On account of its extremely small size it is practically impossible to make out the exact manner of its origin;

whether it is single from the first or is formed by the union of several granules such as are seen at the poles of the previous mitosis (fig. 15) is a question which must remain in doubt. The cell shown in fig. 18 seems to favor the latter interpretation; at the upper pole there appears to be a small group of granules, while at the lower pole the centrosome is larger and distinctly single.

The centrosomes increase rapidly in size. At very late anaphase they are very conspicuous, and the surrounding radiations form a striking system extending through the greater part of the cell (fig. 19). At telophase the rays become short and faint. The centrosomes are still growing, and in some cases may already show indications of division (fig. 20, upper centrosome).

Third spermatogenous mitosis.—There are now 4 cells in each spermatogenous group, and conspicuous in the cytoplasm of each cell (fig. 21) is the centrosome formed during the anaphase of the preceding mitosis. This centrosome undergoes division at once (figs. 22, 23), in fact this process is often seen beginning during the previous telophase (fig. 20). The two daughter centrosomes rarely diverge from one another. In two or three cells they had moved apart to a distance equal to several times their own diameter, and in one uncertain case they appeared to have reached approximately polar positions. As a rule, however, they degenerate in the cytoplasm without performing any further function. At late prophase and metaphase they can often be made out in the cell (fig. 24), but they bear no relation to the spindle poles, which are at first rather indefinite, as in the first and second mitoses. The persistence of faint radiations about them helps to make their identification sure. During anaphase they usually lie in the cytoplasm at the side of the spindle (fig. 25). The cell shown in fig. 26 contains two pairs of minute granules with very faint rays; since this was the only case of the kind observed, it is impossible to say what it may mean, but it is probable that the two centrosomes which ordinarily degenerate at once have here moved apart and divided again. This renders more certain the interpretation placed upon the paired bodies in figs. 24 and 25. They are doubtless to be identified with the "blepharoplastoid" of SHAW, and are in reality the non-functioning centrosomes.

During anaphase a new centrosome appears at each spindle pole, exactly as in the second mitosis, and behaves in a wholly similar fashion in the subsequent stages. When first discernible it is extremely minute (fig. 25), but very rapidly becomes larger (fig. 26). This formation of new centrosomes after the failure of the old ones is a feature of considerable interest, and will be touched upon again in the discussion.

The division of the centrosome occurs during the telophases, but not always at exactly the same stage, as figs. 27 and 28 show. In fig. 27 the lower centrosome is elongating and the upper one beginning to constrict. In fig. 28 the lower one is still spherical, while the upper one is almost completely divided.

Fourth spermatogenous mitosis.—In the interval between the third and fourth mitoses the centrosomes gradually move apart (figs. 29–31). In view of the rôle which they are to play, they may now be called the blepharoplasts. As they diverge, a delicate central spindle remains between them. The radiations on the side toward the nucleus become stronger, and at the stage shown in fig. 31 form two conspicuous cones of spindle fibers with the blepharoplasts at their apices. The rays extending in other directions are not so well developed as in the previous mitoses.

A marked change now begins in the blepharoplasts. They enlarge, develop one or more internal vacuoles, and become irregular in outline (figs. 31, 32). At late anaphase this process has gone on still farther (fig. 33), and at telophase they may be seen breaking up to several irregular pieces (fig. 34).

Metamorphosis of the spermatid.—The transformation of the spermatid into the spermatozoid seems to take place rather rapidly. The fragmentation of the blepharoplast, begun during the telophase of the last mitosis, continues until a considerable group of pieces has accumulated (fig. 35). These soon take the form of an irregular, lumpy rod, which lies close to the nucleus or against it (fig. 36). A later stage is shown in fig. 37; in this cell, which is noticeably larger than those of figs. 35 and 36, the nucleus has begun to undergo a change in shape which will finally result in the spiral form of the sperm, and the blepharoplast, in close union with it, has formed nearly one complete turn.

As the blepharoplast grows in length it gradually becomes more uniform in thickness without passing through such a regular beaded stage as is seen in *Equisetum*. Our preparations did not permit a more detailed study of this growth, nor was the time of the first appearance of the cilia determined. The blepharoplast often shows a double structure (fig. 37), traces of which are visible in the mature sperm (fig. 42, at middle). SHAW (**7**) believed this to be an appearance due to the U-shaped cross-section, an idea which is not supported by the present study.

A more advanced stage in the spiral growth of the nucleus and the blepharoplast is shown in side view and in cross-section in figs. 38 and 39. The blepharoplast grows out freely beyond one end of the crescentic nucleus, a feature again clearly brought out in fig. 40, which represents a cell in which the metamorphosis is about half completed. Cilia are easily made out at this stage. As the transformation continues the nucleus and blepharoplast become more closely compacted and are soon very difficult to distinguish.

When the sperm escapes from the spore the coils, about 8 in number, are rather closely wound (fig. 41). The first three or four anterior coils are made up of blepharoplast only and bear no cilia. The remaining coils are composed of both blepharoplast and nucleus and bear cilia upon all but the most posterior regions. The large vesicle, held in the posterior coils, contains the cytoplasm of the spermatid with its inclusions, such as an occasional starch grain and other disorganized material of undetermined nature (figs. 37–41).

As the sperm swims about, it enlarges through the absorption of water, and when it reaches a denser medium, such as the gelatinous material about the megaspore, the coils become more widely separated from each other. Such a sperm, fixed over osmic fumes, is shown in fig. 42. It has a length of 50 μ, while the newly escaped sperm shown in fig. 41 measures but 15.3 μ.

Discussion

The subject of the morphological nature of the blepharoplast was discussed fully in the writer's paper on *Equisetum* (SHARP **6**), to which the reader is referred. Two extracts will suffice to make clear the conclusions reached.

> Although limited to a single mitosis in the antheridium, the blepharoplast [of *Equisetum*] retains in its activities the most unmistakable evidences of a centrosome nature, and at the same time shows a metamorphosis strikingly like that in the cycads. In thus combining the main characteristics of true centrosomes with the peculiar features of the most advanced blepharoplasts, it reveals in its ontogeny an outline of the phylogeny of the blepharoplast as it is seen developing through bryophytes, pteridophytes, and gymnosperms, from a functional centrosome to a highly differentiated cilia-bearing organ with very few centrosome resemblances [p. 107].
>
> The activities of the blepharoplast in *Equisetum*, taken together with the behavior of recognized true centrosomes in plants and analogous phenomena in animals, are believed to constitute conclusive evidence in favor of the theory that the blepharoplasts of bryophytes, pteridophytes, and gymnosperms are derived ontogenetically or phylogenetically from centrosomes [p. 113].

Let us now turn to the case of *Marsilia*. We have seen that a centrosome first appears at each spindle pole during the anaphase of the second spermatogenous mitosis, and later divides only to degenerate without performing any further function. A new centrosome then appears in the same manner at each pole during the anaphase of the third mitosis, divides, and occupies the spindle poles through the fourth mitosis, and in the spermatid functions as the blepharoplast. This corresponds in the main with SHAW'S (**7**) description, but that writer failed entirely to see the extensive achromatic structures and the intimate relation they bear to the body in question. Had he done so, it is difficult to understand how he could have failed to recognize the homology of the centrosome and the blepharoplast.

The foregoing features constitute the strongest arguments in favor of the centrosome nature of the blepharoplast. We have as yet found no other case in plants where they are emphasized in so striking a fashion. The body divides at each mitosis and forms the center of an achromatic system unmistakably the same as that accompanying true centrosomes in alga and animal cells. The theory that this is more than mere resemblance and is due to homology surely has a better basis in observed fact and is far simpler than the assumption that a special cilia-bearing organ has taken on characters corresponding in all details to those of centrosomes and has extended itself to three cell generations.

To the present writer it seems clear that we are here dealing with an organ which is gradually passing out of the life history. The farther we pass back from the last spermatogenous mitosis the more indefinite its behavior becomes. The centrosome appearing in the third mitosis is intimately concerned in the formation of the achromatic figure for the fourth mitosis, and before the latter is complete the centrosome has already begun to undergo the peculiar transformation of the blepharoplast. The centrosome appearing at the second mitosis later divides, but only occasionally goes farther. In the first mitosis there seems to be still an abortive start in the formation of a centrosome at anaphase (fig. 15), but no definite body is organized. Even in the earlier mitoses of the male gametophyte a system of rays suggests the presence of a dynamic center at each spindle pole, though no centrosome is present (fig. 4).

These considerations, taken together with other instances in which centrosomes have been reported in several generations of spermatogenous cells (bryophytes), and the large number of cases in which they are limited to the last mitosis (*Equisetum*, *Nephrodium*, cycads), have only served to strengthen our formerly expressed opinion that centrosomes have been partially or wholly eliminated from the early spermatogenous cells, and are retained in so many forms only at the end of the series because of the very important biological function they there perform—the bearing of cilia. They are finally lost altogether when the change from motile to non-motile sperms occurs. Just such a progression as this is seen in passing upward through the bryophytes, pteridophytes, and gymnosperms, and *Marsilia* shows a very instructive stage in the process.

A feature of special interest is the degeneration of the *Marsilia* centrosome just before the third spermatogenous mitosis, and the formation of a new one at each spindle pole. This was also reported by SHAW (7), while BELAJEFF (3) thought there was no break in its continuity after the time of its first appearance. As stated in the description, our material shows at this point some variability, and it is of a sort which tends to reconcile the two earlier accounts. In the majority of cases degeneration begins directly after the

centrosome has divided. In some cases, however, the daughter centrosomes diverge somewhat, and very rarely they may reach polar positions. Although we have observed no metaphase figure of the third mitosis with undoubted centrosomes at the poles, it is nevertheless probable that further search would reveal such cases. It is thus possible that both SHAW and BELAJEFF were correct in their interpretations, that they were dealing with two lots of material showing different behavior at this point.

This is apparently a stage in the life history where the centrosome may be seen in the act of dropping out through failure to carry out its function. A new one forms at each spindle pole for the same reasons that one is developed at the preceding mitosis, where it has been entirely lost from the earlier phases, though as yet it is impossible to determine the nature of these reasons. Since the variable behavior indicates that the organ in question is in all probability a disappearing one, and since there is no organ other than a centrosome which we should expect to see being eliminated from spermatogenous cells, the lack of continuity, if it argues at all, argues for the centrosome nature of the blepharoplast rather than against it.

The conclusions reached as the result of the present investigation are necessarily the same as those stated in the writer's paper of 1912 and cited at the beginning of this discussion. *Marsilia* is even more convincing than *Equisetum* in showing the direct derivation of an advanced cilia-bearing organ from a functional centrosome. Since there is every reason to believe that the blepharoplasts of bryophytes, pteridophytes, and gymnosperms are homologous structures, it follows that they are all "ontogenetically or phylogenetically centrosomes."

Summary

1. In the first spermatogenous mitosis there is present at each spindle pole a dense region with radiations, but no centrosome.

2. During anaphase of the second mitosis a centrosome develops at each spindle pole and at telophase divides to two daughter centrosomes. These only rarely develop farther; they usually degenerate at once in the cytoplasm.

3. In the third mitosis a centrosome develops at each spindle pole at anaphase exactly as in the second mitosis, and during telophase or later divides to two daughter centrosomes.

4. These daughter centrosomes, which may now be called blepharoplasts, move apart and occupy the spindle poles through the fourth or final mitosis.

5. The centrosomes are at all times accompanied by extensive radiations, which in the fourth mitosis give rise to the achromatic figure. When the centrosome divides there is present a central spindle and amphiaster as in animal cells.

6. Before the fourth mitosis is completed the blepharoplast becomes vacuolate and breaks up to a number of fragments. In the spermatid these form a band which elongates spirally in close union with the nucleus and bears the cilia.

7. The evidence afforded by *Marsilia*, together with that gained from other plants and certain animals, is believed to show conclusively that the blepharoplasts of bryophytes, pteridophytes, and gymnosperms are derived ontogenetically or phylogenetically from centrosomes.

The writer is greatly indebted to Professor JOHN M. COULTER for placing at his disposal the facilities of the Hull Botanical Laboratory.

UNIVERSITY OF CHICAGO

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EXPLANATION OF PLATES XXXIII AND XXXIV

All figures were drawn at the level of the stage with the aid of an Abbé camera lucida, figs. 1–11 under a Spencer achromatic objective 2 mm. N.A. 1.30 with Zeiss compensating ocular 4, and figs. 13–42 under a Zeiss apochromatic objective 2 mm. N.A. 1.40 with compensating ocular 18. They have been reduced one-half in reproduction, and now show magnifications as follows: figs. 1–11, ×368; figs. 13–42, ×1400.

PLATE XXXIII

FIG. 1.—Microspore at time of liberation from sporocarp: starch grains in cytoplasm.

FIG. 2.—First mitosis in microspore, cutting off prothallial cell (wall 1).

FIG. 3.—Prothallial cell completed.

FIG. 4.—Second mitosis in microspore, forming wall 2 (fig. 8).

FIG. 5.—Third mitosis in microspore, forming walls 3.

FIG. 6.—Fourth mitosis in microspore, forming walls 4.

FIG. 7.—Fifth mitosis in microspore, forming walls 5.

FIG. 8.—Diagram to show sequence of wall formation: the two primary spermatogenous cells marked with nuclei.

FIG. 9.—Two primary spermatogenous cells enlarged.

FIG. 10.—Two-celled stage.

FIG. 11.—Eight-celled stage.

FIG. 12.—Sixteen-celled stage (spermatids).

FIG. 13.—*First spermatogenous mitosis:* late prophase; spindle poles indefinite.

FIG. 14.—Anaphase: cytoplasm denser about poles.

FIG. 15.—Late anaphase: dense regions and radiations present at poles, but no definite centrosomes.

FIG. 16.—Telophase: remnants of polar radiations visible.

FIG. 17.—*Second spermatogenous mitosis:* late prophase; cytoplasm becoming dense and granular at poles of spindle.

FIG. 18.—Anaphase: centrosomes present.

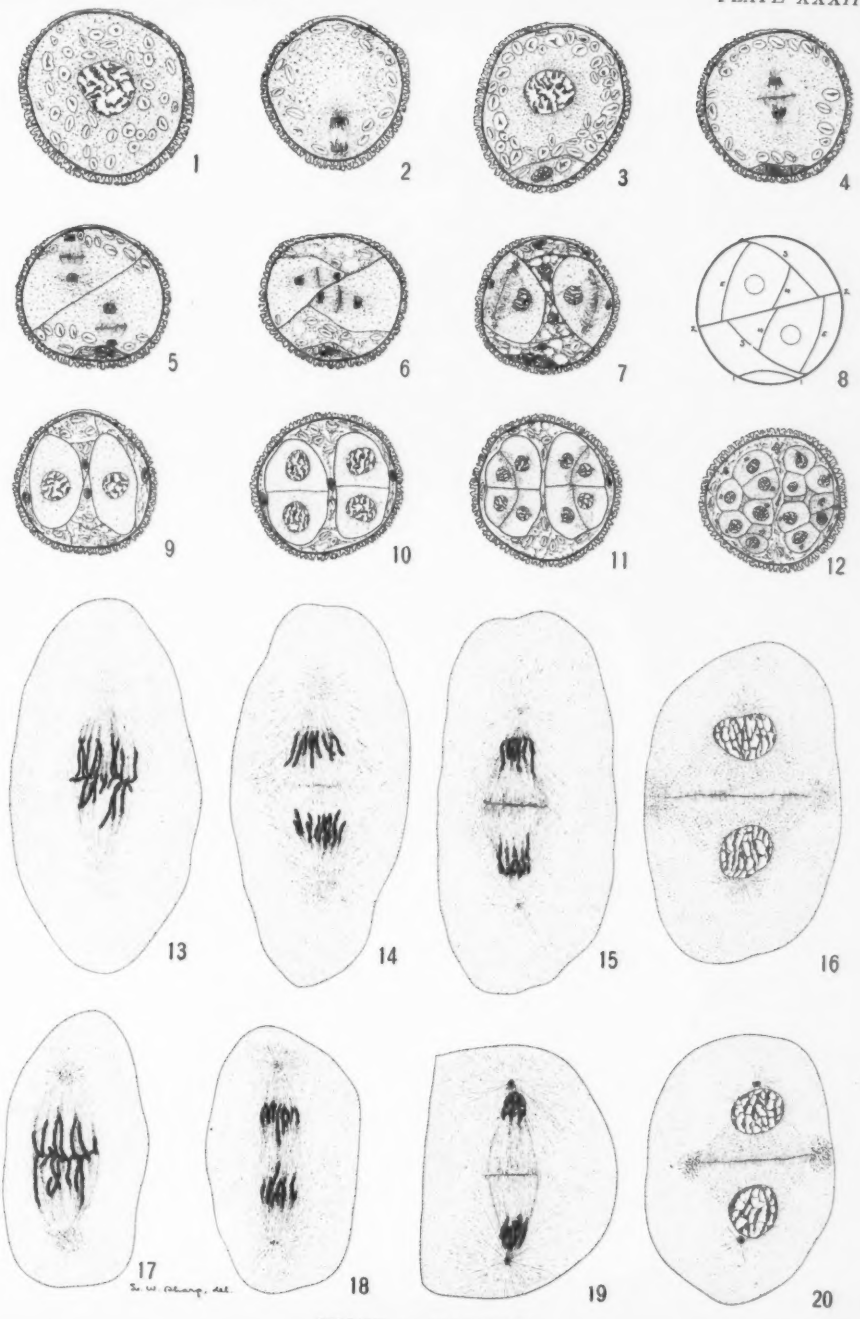
FIG. 19.—Late anaphase: centrosomes and radiations prominent.

FIG. 20.—Telophase: centrosome at upper pole beginning to divide.

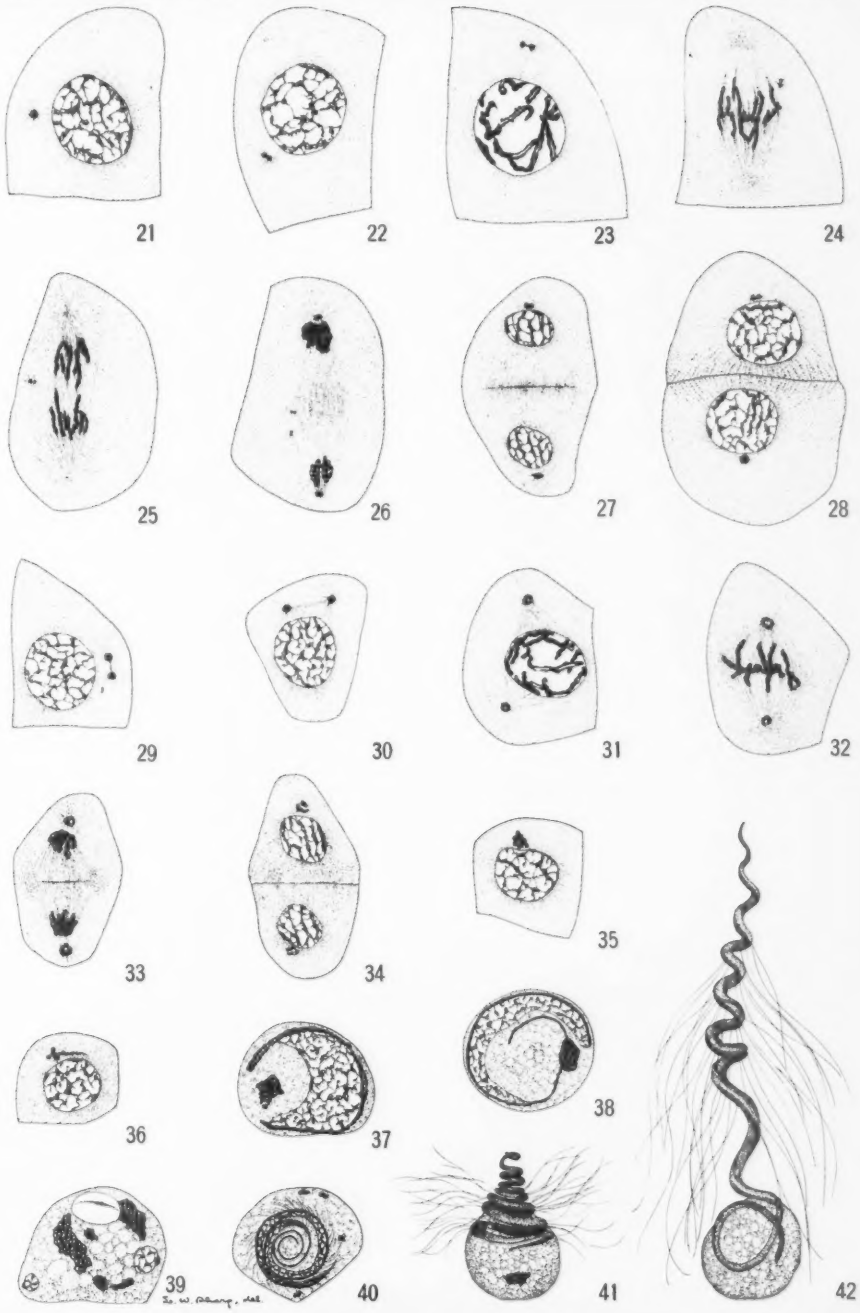
PLATE XXXIV

FIG. 21.—Cell of four-celled stage: centrosome undivided.

FIG. 22.—The same: centrosome divided.



SHARP on MARSILIA



SHARP on MARSILIA

FIG. 23.—*Third spermatogenous mitosis:* prophase.

FIG. 24.—Late prophase: centrosomes disorganizing in cytoplasm.

FIG. 25.—Anaphase: old centrosomes disorganizing; newly formed centrosomes at poles.

FIG. 26.—"Tassement polaire" stage: old centrosomes have undergone division; new centrosomes greatly enlarged.

FIG. 27.—Telophase: centrosomes beginning to divide.

FIG. 28.—Telophase: division of upper centrosome nearly completed; lower one undivided.

FIG. 29.—Cell of eight-celled stage: centrosomes (blepharoplasts) moving apart.

FIG. 30.—The same, more advanced.

FIG. 31.—*Fourth spermatogenous mitosis:* prophase; spindle forming from radiations; blepharoplast becoming vacuolate.

FIG. 32.—Late prophase: blepharoplast more irregular.

FIG. 33.—Late anaphase.

FIG. 34.—Telophase: blepharoplast breaking up.

FIGS. 35, 36.—Spermatids: blepharoplast has fragmented further and is beginning to form band.

FIG. 37.—Early stage of metamorphosis of spermatid: blepharoplast shows double structure in certain parts.

FIG. 38.—Later stage: blepharoplast grows out freely beyond one end of nucleus.

FIG. 39.—Cross-section of cell in same stage: sections of nucleus with closely appressed blepharoplast at right and left; starch and other disorganized material in cytoplasm.

FIG. 40.—More advanced stage: cilia growing out from blepharoplast.

FIG. 41.—Spermatozoid shortly after escape from microspore: cilia only on middle coils; length 15.3 μ.

FIG. 42.—Spermatozoid in gelatinous material about megaspore, fixed over osmic fumes; length 50 μ.

THE PLANT SUCCESSIONS OF THE HOLYOKE RANGE

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 198

EDITH A. ROBERTS

(WITH MAP)

Introduction

The Holyoke Range lies well within the eastern deciduous forest region with the climatic plant formation of the mesophytic deciduous climax type made up of *Acer saccharum* (sugar maple), *Fagus grandifolia* (beech), and *Tsuga canadensis* (hemlock). The range is located nearly in the center of the Connecticut valley, which crosses the state of Massachusetts from north to south and varies from 100 to 1200 feet in elevation. The many topographical features offer opportunity for the study of the development of the vegetative cycles terminating in the climax forest of central Massachusetts.

A few isolated portions which have been uncut for over 250 years furnish evidence as to the climax, while the repeated cutting in other places gives excellent opportunity to study the development of the so-called "secondary succession" (1), a study which will of necessity be more valuable as the work of reforesting increases, especially in the New England states, where the future forests will for the most part be of that type.

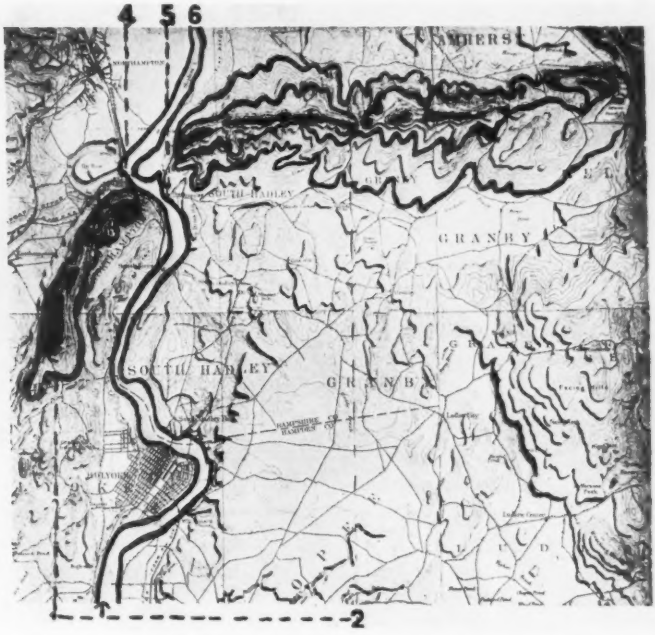
The purpose of the work is to determine the varying lines of biotic successions leading to the present climax in this region, and in a later paper to determine the relationship of the factors which are influencing these successions.

The region is typical of the central portion of the state and the range represents a natural unit which, owing to its direction (see map), offers opportunity to study north, south, east, and west slopes, with their variations in succession.

The work was begun at the suggestion of Dr. HENRY C. COWLES, of the University of Chicago, and I wish to express my thanks for his suggestions and interest in the work. I wish to thank Miss MIGNON TALBOT, of Mount Holyoke College, for the material on

the topography and physiography of the region, and Miss SARAH J. AGARD, of the botany department, for identification of uncertain species.

The nomenclature of the pteridophytes and spermatophytes is that of the seventh edition of GRAY'S *Manual*.



MAP.—1, Mount Tom Range; 2, Mount Holyoke Range; 3, Holyoke Range; 4, Nonotuck; 5, Titan's Pier; 6, Connecticut River.

Topography and physiographic history

The Holyoke Range is situated in the western central part of Massachusetts in lat. 42° N., long. 70°30′ W., in an old river valley. The range varies in elevation from 100 feet to 1200 feet and is 10 miles in length.

The valley was carved out by stream erosion upon a great thickness of sandstone, conglomerates, and shales with interbedded lavas; the main sheet of which, and the one which caps the ridges,

is the Holyoke diabase. These Triassic rocks were later subjected to tilting, warping, and faulting, and these processes, together with stream erosion, resulted in the formation of the "trap" ridges which stand above the valley floor with steep cliffs facing the west or the north, as the case may be, and more gentle slopes on the east and the south, slopes that are practically that of the dip of the rocks. These cliffs are in places 600 feet high and in others are almost buried by the accumulation of talus and glacial débris. There are numerous faults running north and south, in general crossing the Holyoke Range at right angles and running almost parallel with the Mount Tom Range.

During the ice age the ice sheet passed over the region and left much glacial material on the north side of the range. As the ice retreated north a lake was formed here and another one on the south side. The one north of the range was called the Hadley Lake and the one south, the Springfield Lake.

The Hadley Lake found an outlet between Nonotuck and Titan's Pier (see map). Today the area is drained by the Connecticut River, which doubtless has occupied different portions of the lake bed, but now is cutting close to the east side of the Mount Tom Range (see map).

The region is being acted upon but little by stream erosion, as the streams are of small size. On the south side of the Mount Holyoke Range there formerly were 20 streams originating at an elevation of 400–500 feet, while on the north side there were 6 at that height. The many streams on the south side of the range were doing active erosion work along the fault lines, but the frequent deforestation has been instrumental in exhausting the streams, and as a result there are many ravines, young topographically but quite old floristically.

On the north side of the Mount Holyoke Range there are wide crevices in the cliff face due to the presence of faults, but below the cliff face the mountain side presents a uniform mass of talus and glacial débris. Along the talus below the wide crevices there is always a greater amount of moisture, where more of the "run off" on the north side of the range sinks into the talus than along the talus at the foot of the unbroken cliff face.

There is little bare rock exposed except on the cliff faces and at the edges of the highest peaks; there weathering is playing an active part. Small and large flakes of the trap rock are being split from the face. A great many of them pile up at the top of the talus slope and furnish splendid agents for catching the finer material which is washed down.

The vegetation is playing an active part in changing the physiographic features of the region.

Classification of successions

The initial biotic vegetative cycles are so determined by the original xerophytic and hydrophytic habitats, that I have classified the xerarch (1) and hydrarch successions in topographic terms as follows:

I. Xerarch successions: (1) trap slope successions; (2) trap cliff successions; (3) talus successions.

II. Hydrarch successions: (1) ravine successions; (2) brook successions.

All the region except the brooks has passed through several of the successions leading to the climax forest, and a small area is now in the beech-maple climax, which is the culminating stage of the region, while a little to the west of the range the hemlock forms the climax. There is, however, in this region some indication of the hemlock coming in as a climax type.

It is doubtful if there is any climax representing that of the so-called primary succession, which might well be called the initial succession. The region represents a third or fourth attempt to develop a climax forest, as do most of the New England forest areas. These successions have been called secondary successions, but might better be called repetitive successions, because the deforestation causes the area to revert to an aspect which is a combination of a former succession with the successions which ordinarily follow it. The term "secondary" does not carry with it the idea of more than one attempt at repetition, while "repetitive" indicates no limit in the number of attempts.

Mount Tom has been a state reservation for 10 years, and since then has been free from the retarding and retrogressing factor, man.

This biotic influence has interrupted successions on every topographic type, chiefly in the following ways: cutting, with or without burning, followed by cultivation, pasturing, or permitting the area to become of economic value without assistance from man.

This always retards the development of the area temporarily, although it soon assumes the aspect of some previously established type, modified by the interpolation of certain species, and it retains, unless burned over, remnants of the previously established types, especially among the herbs. These are of aid in the determination of the history of the region in regard to the activities of men and plants.

The plants are listed here under the great groups, making it possible to bear out NICHOLS' (3) statement that "species in groups of comparatively recent evolutionary derivation are far more restricted in range than species in groups of more recent origin." The spermatophytes are again divided into trees, shrubs, and herbs, to indicate more clearly the difference in biotic influence.

Xerarch successions

TRAP SLOPE

There is an east face and a south face; the former belongs to the Mount Tom Range, which has been a state reservation for 10 years, and which, it is hoped, will some day afford an opportunity of seeing in this region a climax forest of some extent.

There is no difference in the two slopes aside from the presence on the south face of more ravines; in these ravines cutting has ceased, as deforestation followed by fire has caused the drying up of streams, leaving the ravines young topographically. The entire region has been cut over within the last 25 years. At the top the vegetation is again getting a foothold on the rock outcrop, except at the edge, along the fault lines; here there is young tree growth, in which can be found old stumps of red oak three feet in diameter, indicating how far the region had progressed in its development.

On the rock outcrop are found the following:

Spermatophyta: Herbs.—*Carex rosea*, *Aquilegia canadensis*, *Corydalis sempervirens*, *Arabis Drummondi*, *Saxifraga virginiensis*, *Arctostaphylos Uva-ursi*, *Cardamine parviflora*.

Pteridophyta: *Woodsia Ilvensis*, *Selaginella rupestris*.

Bryophyta: *Umbilicaria* sp., *Ceratodon purpurea*, *Physcia* sp.

A few feet below the rock outcrop are found the following:

Spermatophyta: Trees.—*Juniperus virginiana*, *Carya alba*, *C. ovata*, *Quercus alba*, *Q. rubra*, *Q. Prinus*. Shrubs.—*Quercus prinoides*, *Amelanchier canadensis*, *Pyrus arbutifolia*, *Cornus circinata*, *Vaccinium stamineum*, *V. cassinoides*. Herbs.—*Maianthemum canadense*, *Polygonatum biflorum*, *Hypoxis hirsuta*. New ferns are *Aspidium marginale*, *Polypodium vulgare*, and *Polystichum acrostichoides*.

Where the faults are at right angles to the range, the rock cliff has been worn away and the edges take on a rounded form. Here the trees have been established longer and are about three inches in diameter. There is found the same grouping as is found a hundred feet below the top of the trap rock slope, with the addition of *Castanea dentata* and *Acer saccharum* as seedlings. The new shrubs are *Diervilla Lonicera* and *Viburnum acerifolium*, while the spermatophytic herbs are *Uvularia perfoliata*, *Thalictrum dioicum*, *Hepatica triloba*, *Anemone quinquefolia*, and *Aralia nudicaulis*. The ferns are *Pteris aquilina*, *Asplenium Trichomanes*, and *Cystopteris bulbifera*.

The lower half of the slope, though cut at the same time, has advanced much more rapidly. Wherever there is a trap rock outcrop the bryophyte and pteridophyte vegetation is found, and about it the spermatophytes just mentioned, but the trees are larger and the following additional species have come in: *Fagus grandifolia* as a seedling, with occasional plants of *Tilia americana* and *Fraxinus americana*. The shrubs are *Hamamelis virginiana*, *Dirca palustris*, *Cornus florida*, and *Viburnum dentatum*. Characteristic spermatophytic herbs are *Arisaema triphyllum*, *Habenaria Hookeri*, *Habenaria bracteata*, *Actaea rubra*, *Pyrola elliptica*, *Lysimachia quadrifolia*, *Orobanche uniflora*. The ferns are *Pteris aquilina*, *Polystichum acrostichoides*, *Dicksonia punctilobula*, and *Asplenium acrostichoides*.

The base of the trap slope has now on it every type of repetitive succession except that of cut-over beech forests. Places untouched for the longest time show the dominance of chestnut. Red oak and

white oak stumps 4 feet and 5.5 feet in diameter indicate that the region was allowed to pass at least through the oak succession, and chestnut 2 feet in diameter with hard maple 1 inch in diameter show that it is the day of the chestnut with the promise of hard maple later. Old landmarks of hard maple and chestnut give evidence of a previous attainment of that stage of succession, which appears to be the temporary climax of the east and south slopes.

TRAP CLIFF

The cliff is of greater height on the west side of Mount Tom than on the north side of Mount Holyoke. The numerous faults on Mount Holyoke run at right angles to the range, and the more active erosion along the fault lines increases the amount of talus. This, in addition to the glacial drift deposited on the north side, accounts for the talus reaching the top of the mountain and burying the cliff face, except for short spaces between the fault lines. On Mount Tom the faults are fewer and run parallel with the cliff face, and the glacier left no deposit except at the Nonotuck end (see map).

A lichen flora, yet undetermined, is established on most of the cliff, *Umbilicaria* playing a conspicuous part. The rock flakes off so rapidly that it is doubtful if any later vegetation is established. Often before the lichens are established the rock flakes off and is added to the talus below. The talus is made up of large flakes with or without lichens upon them.

The crevices and shelves afford a more permanent foothold and conifers have become established here, so that from a distance the mountain side appears to be rather well covered with trees.

The following species are found in crevices, and on shelves of the east-facing cliff: Spermatophyta: Trees.—*Juniperus virginiana*, *Pinus Strobus*, *Pinus resinosa*, *Tsuga canadensis*. Herbs.—*Saxifraga virginiensis*, *Corydalis sempervirens*, *Campanula rotundifolia*. Pteridophyta: *Woodsia Ilvensis*, *Asplenium Ruta-muraria*. Bryophyta: *Hedwigia albicans*, *Grimmia apocarpa*.

The cliff represents, if do any of the regions, the first of the initial successions. The first stages in the group of initial successions on the north face and the east face are the same, but the second stages are different. The many shelves found on the east side offer

a place for more rapid accumulation of soil; junipers, pines, and grey birches come in, while on the north face *Tsuga canadensis* gets a foothold in the crevices.

The pines and the hemlock seem to represent a temporary climax until the edaphic situation becomes altered.

TALUS SUCCESSION

At the west side of the Mount Tom Range the talus is made up of trap flakes alone, while on the north side of the Mount Holyoke Range it is composed of trap and glacial drift. In each case trees and undergrowth are established on the entire talus except where patches of rapidly weathering rock have covered all but tree growth; in such places birch or butternut may be seen growing in the midst of an island of trap chips. At the base of Mount Holyoke, where the glacial drift is associated with trap chips, the soil is far more stable and is covered with herbaceous forms.

Shrubs and vines advance up the slope at the base of the cliff, with the assistance of a little lichen or moss growth. At the top of the talus, which is made up of clean trap chips, an interesting advance is made by the plants with creeping stems and rootstocks, *Rhus Toxicodendron*, *Psedera quinquefolia*, and *Vitis aestivalis*.

The talus on the north side of Mount Holyoke presents an almost unbroken slope except at the top. As the fault lines extend across the trap face, short ravines have been formed at the head of the ravines of the trap slope. Here the drainage divides to the north and south and the north face receives more moisture below these short ravines. This unequal amount of moisture together with the greater amount of shade, due to the projecting sides of the trap ravines, affects the vegetation for about 50 feet along each fault, and below this the talus assumes a uniform aspect.

In a short ravine facing north are found: Spermatophyta: trees over a foot and a half in diameter, *Tsuga canadensis*, *Betula alba*, *B. lutea*, and *B. lenta;* trees about an inch in diameter, *Ostrya virginiana*, *Quercus rubra*, *Q. alba*, and *Carya ovata;* there are a few seedlings of *Acer saccharum;* and scattering shrubs of *Hamamelis virginiana*, *Acer spicatum*, and *Viburnum acerifolium* are found. The spermatophytic herbs are *Maianthemum canadense*,

Senecio aureus, *Polygonatum commutatum*, *Aralia nudicaulis*, and *Mitchella repens*. The Pteridophyta are *Adiantum pedatum* and *Lycopodium lucidulum*.

Where the slope is uniform are found: *Betula lenta*, *B. alba*, *Juglans cinerea*, *Fraxinus americana*, *Quercus rubra*, *Q. alba*, *Q. Prinus*, *Carya alba*, and *Castanea dentata*, all over a foot in diameter. Old stumps of *Tsuga canadensis* and isolated specimens of *Pinus rigida* and *Pinus Strobus* tell of the history of the slope. *Acer saccharum* of small size prophesies the future of the slope if it is left to itself. The following shrubs, *Kalmia latifolia*, *Acer spicatum*, *Cornus florida*, evidence better conditions for growth, as do also the herbs *Uvularia perfoliata*, *Trientalis americana*, *Trillium erectum*, and *Maianthemum canadense*. The Pteridophyta are represented by *Adiantum pedatum*, *Osmunda cinnamomea*, *Dicksonia punctilobula*, and *Polystichum acrostichoides*.

The chestnut–red oak–white oak–hickory stages seem to be telescoped (2) on the north side, while on the south face the stages are distinct.

The talus on the north side below this grouping has much hard maple and many young beech trees 10 inches or more in diameter. Whether it is or is not a question of more frequent deforestation on the one side than on the other, it is true that the beech is far more common on the north side. In some places there are beech trees three feet in diameter with an undergrowth of young beech and hemlock; while on the east-facing talus and on the south-facing trap rock, as well as on the north, old stumps of hard maple and chestnut three feet in diameter are common, but there is no indication of beech coming in other than occasional one-inch saplings.

Herbs show a quicker reaction to environment and are more rapid indicators of changing conditions than trees. The spermatophytic herbs found near the base of the slope are *Uvularia perfoliata*, *Erythronium americanum*, *Trillium sessile*, *T. erectum*, *T. cernuum*, *Orchis spectabilis*, *Habenaria bracteata*, *Epipactis repens*, *Actaea rubra*, *Dicentra Cucullaria;* and the Pteridophyta, *Phegopteris Dryopteris*, *P. polypodioides*, *P. hexagonoptera*, *Adiantum pedatum*, *Aspidium spinulosum*, *Cystopteris fragilis*, and *Botrychium virginianum*.

There is an indication of the hemlock coming in twice in the succession, first in the early stages of the ravines as a temporary climax, and later at the climatic climax of the region as shown in the successions on the north talus slope. The white pine does much the same thing, forming a temporary climax on the east-facing cliffs and a temporary climax on the lake bottom sands, which are at the foot of the talus slope. There are many places just south of the range along the old lake shore where the pine remains established for some time. It looks as if the region had reached the pine stage many times; now conditions are such that the region is advancing a stage and oaks and chestnut are beginning to get a foothold. The accompanying diagram in a general way indicates the natural successions and the effect of repeated deforestation.

Hydrarch successions

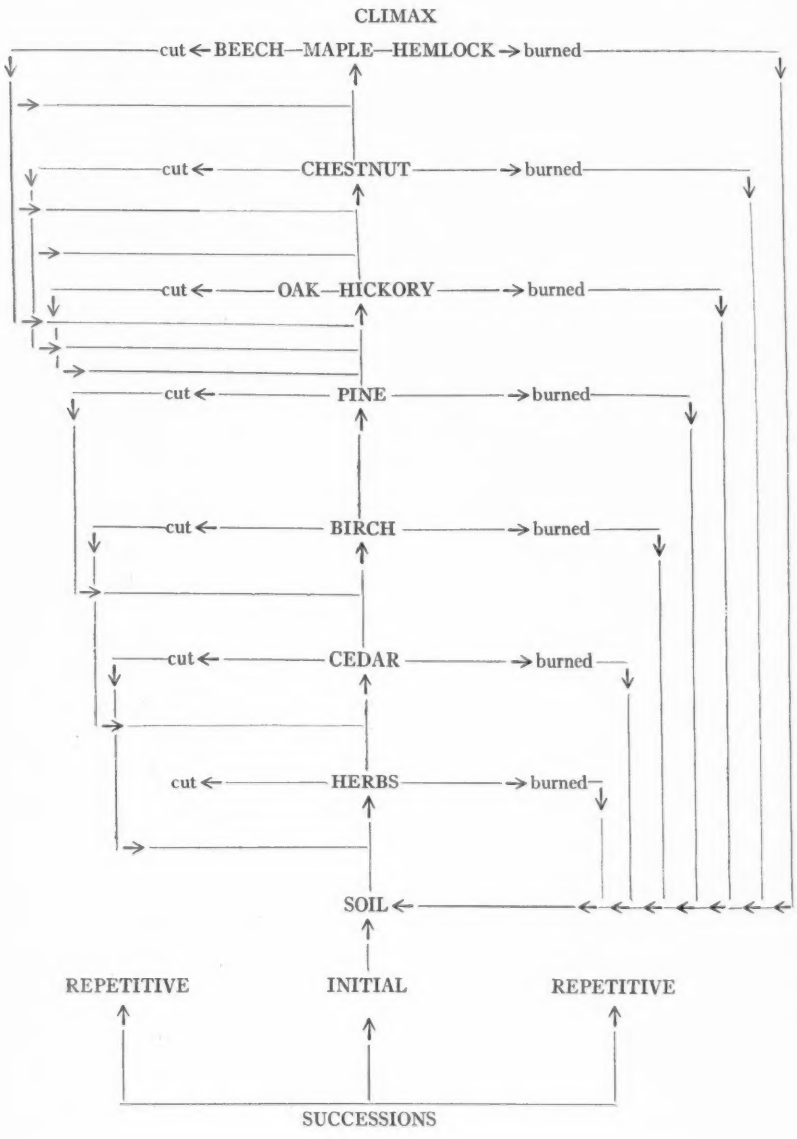
RAVINE SUCCESSIONS

The ravines parallel to the Mount Holyoke Range and the ravines on the south trap face of Mount Holyoke are to be considered.

The parallel ravines on Mount Tom have been formed by differential weathering and never had any streams in them. The rock sides are perpendicular and have no vegetation but lichens, except for a few crevice plants. The base of the ravine is covered with trap chips among which vines and a few shrubs are getting a foothold.

The ravines on the trap slope are no longer being actively cut. The rapidly repeated deforestation has exhausted many of the streams, so that there are found many ravines young topographically but old floristically. In the early spring the melting snows drain down these ravines. Other ravines are older topographically and have wide sides, which are the same floristically as the adjoining slope of the range at the same level.

In a ravine from which water has recently been withdrawn can be found *Tsuga canadensis*, *Pinus Strobus*, *Juglans cinerea*, *Tilia americana*, *Betula lenta*, *B. lutea*, *Castanea dentata*, *Acer saccharum*, and some very young *Fagus grandifolia*. Time enough apparently


CLIMAX
cut
BEECH—MAPLE—HEMLOCK
burned
cut
CHESTNUT
burned
cut
OAK—HICKORY
burned
cut
PINE
burned
cut
BIRCH
burned
cut
CEDAR
burned
cut
HERBS
burned
SOIL
REPETITIVE
INITIAL
REPETITIVE
SUCCESSIONS

has passed in the ravine formation to permit the passing of the succession to *Fagus grandifolia*.

A young ravine on the south side in which cutting has long since ceased contains many of the same forms showing a slow succession.

THE BROOK

The brooks are fast passing out of existence in the vicinity of the range, so that mention is made only of the plants found in the brook and on its immediate banks. The trees are *Ulmus americana* and *Acer rubrum;* the shrubs, *Alnus incana*, *Benzoin aestivale*, *Ilex verticillata*, *Vitis Labrusca*, *Cornus stolonifera*, and *Dirca palustris;* the herbs, *Thaspium aureum*, *Caltha palustris*, and *Symphoricarpus foetidus*. This is soon followed by a heavy growth of *Carpinus caroliniana*, with *Betula lutea*, *B. lenta*, and *Fraxinus americana*. These pave the way for oaks and hickories.

Summary

1. The region is a mountain range of trap rock.

2. The climax forest of the region is of the beech-maple-hemlock type.

3. The successions may be classified as:

I. Xerarch successions: (1) trap slope successions; (2) trap cliff successions; (3) talus successions.

II. Hydrarch successions: (1) ravine successions; (2) brook successions.

4. The terms initial and repetitive seem to be better than primary and secondary in conveying the idea of often-repeated successions such as are found in a frequently deforested area.

5. The east-facing and the south-facing trap slopes have the same successions. *Castanea dentata* seems to present a temporary climax.

6. The trap cliff doubtless presents an initial succession in which the east and north cliffs have similar first stages, but the second stage on the east is *Pinus Strobus* and *Pinus resinosa*, while on the north it is *Tsuga canadensis*.

7. The combination of weathered rock with glacial drift on the north talus slope affords a better opportunity for the climax formation than does rock alone on the talus east of Mount Tom.

8. Repeated deforestation has prevented all but a small area from reaching the climax.

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HISTOLOGY OF FLAX FRUIT

KATE BARBER WINTON

(WITH FOUR FIGURES)

Flax (*Linum usitatissimum* L.), although grown throughout the temperate zone for its fiber, is valuable as well for its seed, which yields the well known linseed oil, the residue being used as a cattle food. The chaff from the threshing of the seeds, consisting of broken pods and stems with varying amounts of immature and broken seeds, has of late come into the cattle food market under the name "flax bran."

The histology of the fiber is described by VON HÖHNEL,[1] HANAUSEK,[2] and other technical microscopists, and that of the seed by writers on the microscopy of foods and drugs,[3] but the elements of the pericarp appear to have escaped attention except for brief mention by COLLIN and PERROT,[4] with whom the present writer does not entirely agree.

FIG. 1.—Dehiscing fruit with sepals; ×2.

The yellowish pods (fig. 1), 8 mm. in length, are slightly broader than long, with five pointed sepals and a slender pedicel. Each of the five locules is incompletely halved by a false dissepiment, making a 10-celled fruit which dehisces at maturity into ten valves. Each cell contains a single flattened, shining, brown, mucilaginous seed.

CALYX.—The *outer epidermis* consists of longitudinally elongated cells with wavy walls and simple stomata. The cuticle has faint longitudinal striations.

Mesophyll.—Several layers of simple parenchyma cells, through which runs a network of small bundles, form the mesophyll.

The *inner epidermis* is similar to the outer.

[1] Die Mikroskopie der Technisch Verwendeten Faserstoffe. Wien, 2 Aufl. 1905. p. 42.

[2] Microscopy of technical products. Trans. by WINTON. New York. 1907.

[3] See bibliography in WINTON, Microscopy of vegetable foods. New York. 1906. p. 204.

[4] Les résidues industriels. Paris. 1904. p. 202.

PEDICEL.—The *epidermis* is made up of longitudinally elongated rectangular cells with straight, pitted walls. Occasional simple stomata are present.

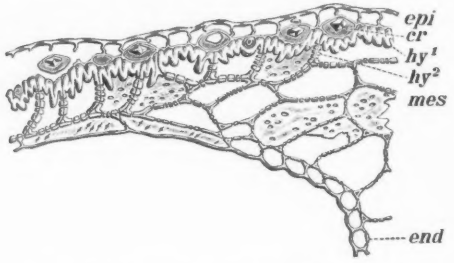

FIG. 2.—Pericarp in cross-section: *epi*, epicarp; *cr*, crystal cells; *hy*¹, projections of hypoderm; *hy*², hypoderm; *mes*, mesocarp; *end*, endocarp; ×160.

Subepidermis.—A few layers of small thin-walled parenchyma form this tissue.

Bast.—The conspicuous elements constituting the bulk of the pedicel are the bast fibers. They are greatly elongated thick-walled cells with occasional characteristic cross-striations resembling joints, and conform in general structure to the bast fibers of the stem, which yield the linen of commerce.

The *xylem* contains spiral and pitted vessels, wood fibers, and parenchyma cells without distinctive features.

None of the tissues of the calyx and pedicel is of especial diagnostic importance.

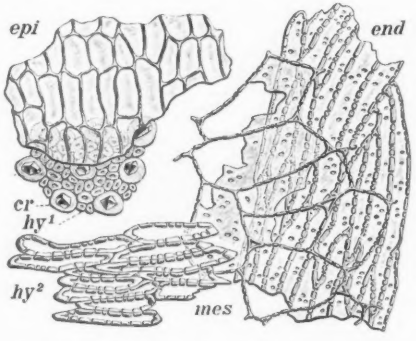

FIG. 3.—Elements of pericarp in surface view: *epi*, epicarp; *cr*, crystal cells; *hy*¹, projections of hypoderm; *hy*², hypoderm; *mes*, mesocarp; *end*, endocarp; ×160.

PERICARP (figs. 2 and 3).—The *epicarp* (*epi*) consists of a single layer of collapsed cells whose outlines are found most easily in surface view. They are frequently longitudinally elongated to about twice their width, have straight thin walls, and occasionally yellowish contents which harden at maturity, retaining the shape of the confining cell walls. COLLIN and

PERROT (*loc. cit.*) describe crystals in this layer, but the writer finds them in an interesting tissue below the epicarp.

Crystal cells (*cr*).—Resting on the hypoderm and more or less separated by its projections is a strikingly characteristic tissue one cell in thickness, consisting of isolated compressed spherical or lens-shaped cells arranged in indistinctly longitudinal rows. The light brown inner and side cell walls are so thickened that the cell contents, consisting of a single monoclinic crystal (about 13 μ), completely fill the lumen. On sectioning, the crystal usually escapes through the thin outer wall.

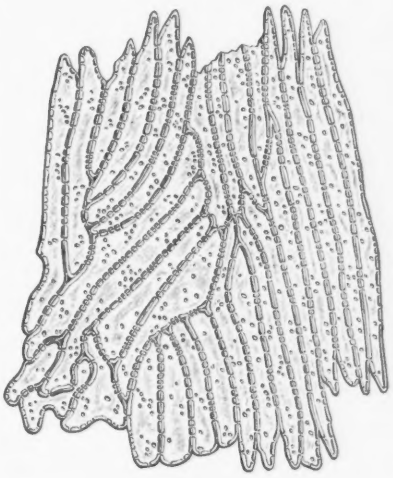

FIG. 4.—Dissepiment in surface view; × 160

The *hypoderm* (*hy*^{1} and *hy*^{2}) is yellowish in color, pitted, and greatly thickened, with numerous projections of the outer wall pushing up under and between the isolated crystal cells. In tangential sections through the outer walls these projections (fig. 3, *hy*^{1}) appear like another layer of small, more or less spherical cells. The cells are transversely elongated over the greater part of the valve, changing abruptly to a longitudinal arrangement at the sutures.

The *mesocarp* (*mes*) varies greatly in thickness. At the thin center of the valve it is frequently lacking, but becomes a thick mass of cells along the juncture with the dissepiment. The cells have slightly thickened pitted walls, except those adjoining the hypoderm, which may be thicker. Cell contents are usually lacking though occasionally small starch grains are present indicating slight immaturity.

Endocarp (*end*).—The single layer of pitted, strongly elongated cells, arranged side by side in groups, is similar to the epidermis of

the dissepiment, with which it forms one continuous tissue, the only noticeable difference being that the cells are somewhat smaller.

DISSEPIMENT (fig. 4).—This transparent papery tissue at once attracts attention, being made up of two parquetry-like epidermal layers of elongated, pitted cells between which is an inconspicuous empty parenchyma. The cells of one epidermis frequently cross those of the other, which at once distinguishes the dissepiment from the endocarp. The walls are approximately straight except at the free edge of the dissepiment, where they become sinuous, acquiring beautiful irregular shapes. The contour of the cell varies greatly with the focus, owing to irregularities of the end walls.

CHARACTERISTIC ELEMENTS.—The tissues which are of chief value in the identification of flax fruit in ground products, such as mixed cattle feed, are the elongated, thick-walled cells of the hypoderm with projections (figs. 2 and 3, hy^1), the accompanying cells each containing a single crystal (*cr*), and the transparent dissepiments with elongated cells (fig. 4), those of the two epidermal layers often crossing at an angle.

All of these tissues are quite different from the elements of any other material likely to be encountered.

WASHINGTON, D.C.

CURRENT LITERATURE

BOOK REVIEWS

The vegetation of Lake Constance

An admirable illustration of the intensive study inspired in his students by SCHRÖTER is found in the elaborate and thorough monograph on the vegetation of the Untersee by BAUMANN.[1] The Untersee is one of the lower arms of Lake Constance on the border of Germany and Switzerland, it being through this arm that the Rhine leaves the lake. After an account of the geology, geography, and hydrography, BAUMANN gives a most interesting account of the different sorts of calcareous deposits, which here take an unusually important part in soil formation, as noted years ago by HONSELL. Calcareous tuffs are formed in extensive amount through the agency of algae. These organisms withdraw carbon dioxide from the calcium bicarbonate in the waters, and the remaining calcium monocarbonate is deposited about the algae as a crust. Later the plants die, leaving only the incrusting masses. In time these processes result in the formation of extensive banks, of which the inner layers are dead, whereas the outer layers contain living algae; these banks, therefore, are precisely comparable to coral reefs. At times the calcareous deposits are in grains, each grain representing the stratified calcareous accumulations about an alga. The Island of Langerain has been formed mostly in this manner. It is thought that these calcareous deposits have been accumulating continuously since the ice age, and they are still accumulating.

The great body of the work is devoted to a detailed study of the species ecology of the characteristic plants. This represents a vast amount of valuable work, which will be of first importance to all students of the vegetation of lakes and swamps. A chapter is devoted to the plant associations, which are of the usual sort for such habitats. Only the larger plants are discussed here, the plankton and the profundal benthos being omitted. The associations are considered under three main heads: the littoral benthos ("Uferflora"), the pleuston, and the "Grenzflora" (that is, the flora between low and high water). These main divisions are of course subdivided. The subdivisions of the littoral benthos from deep to shallow water (also in the successional order) are the Characetum, the Potametum, the Nupharetum, the Scirpetum, and the Phragmitetum. It is of interest to note that these associations are still almost entirely natural, in spite of the many centuries of human occupation of the region. The work closes with a short floristic chapter.—H. C. COWLES.

[1] BAUMANN, EUGEN, Die Vegetation des Untersees (Bodensee), eine floristisch-kritische Studie. pp. v+554. *pls. 15. figs. 31.* Stuttgart: E. Schweizerbartsche Verlagsbuchhandlung. 1911.

MINOR NOTICES

North American Flora.[2]—The first part of volume 10 presents 10 genera of the white-spored series of the tribe Agariceae. The species number 281, of which 39 are new. The largest genus is *Melanoleuca*, with 119 species, 24 of which are new, and 65 transferred from other genera, chiefly *Agaricus* and *Tricholoma*. The other large genera are *Lepiota*, with 88 species, 10 of which are new, and *Venenarius*, with 26 species, 2 of which are new. There are also 3 new species in *Cortinellus*.

The first part of volume 29 presents five of the eight families of Ericales, 281 species being recognized, 50 of which are new. New genera are described in Monotropaceae (*Pityopus*) and Ericaceae (*Therorhodion*, *Oreocallis*, and *Ornithostaphylos*). New species are also described in *Clethra* (7), *Hypopitys* (1), *Pleuricospora* (1), *Newberrya* (1), *Pyrola* (2), *Ramischia* (1), *Chimaphila* (6), *Ledum* (1), *Azalea* (1), *Kalmia* (1), *Kalmiella* (1), *Cassiope* (1), *Andromeda* (1), *Xolisma* (5), *Gaultheria* (10), *Arbutus* (1), *Comarostaphylis* (6), and *Arctous* (1). The large genera of Ericaceae, as now organized, are *Xolisma* (24 spp., mostly from *Lyonia*), *Gaultheria* (24 spp.), *Uva-ursi* (24 spp., mostly transfers), and *Comarostaphylis* (22 spp., mostly from *Arctostaphylos*).—J. M. C.

Icones Bogorienses.—The fourth volume of this work, dealing chiefly with plants of Java and Borneo, is completed by the fourth fascicle,[3] which presents 3 species of Zingiberaceae, one each of Burmanniaceae, Euphorbiaceae, and Ericaceae, and 19 species of Rubiaceae, each species illustrated by a plate. New species are described in *Burmannia* (1), *Antidesma* (1), *Rhododendron* (1), *Lerchea* (1), *Argostema* (3), *Andina* (1), and *Acranthera* (8).—J. M. C.

NOTES FOR STUDENTS

The xeromorphy of marsh plants.—A study of great interest and thoroughness is reported by YAPP,[4] who has for some years been investigating the ecology of marsh plants. He has made an intensive study of the species ecology of *Spiraea Ulmaria*, carrying on many experiments, as well as making many field observations. The fundamental importance of carrying on many such studies cannot be emphasized too strongly. In this species all leaves formed during the first year are glabrous; on older plants the leaves become

[2] North American Flora **10**: part 1. pp. 76, Agaricaceae (pars), by W. A. MERRILL; and **29**: part 1. pp. 102, Ericales, by J. K. SMALL; Clethraceae, by N. L. BRITTON; Lennoaceae and Pyrolaceae, by P. A. RYDBERG; Monotropaceae and Ericaceae, by J. K. SMALL (*Uva-ursi* by LEROY ABRAMS). New York Botanical Garden, 1914.

[3] Icones Bogorienses **4**:239–294. *pls. 376–400.* Leide: Jardin Botanique de l'État. 1914.

[4] YAPP, R. H., *Spiraea Ulmaria* L., and its bearing on the problem of xeromorphy in marsh plants. Ann. Botany **26**:815–870. *pls. 3. figs. 11.* 1912.

progressively hairy from the base to the top. On non-flowering shoots, however, the later leaves, like the earlier, are glabrous. On partially hairy leaves the terminal leaflet is invariably the most hairy, and there is a regular decrease in hairiness downward. Although it is more conspicuous in *Spiraea Ulmaria*, this seasonal periodicity in hair formation was found in many other plants. The lower glabrous leaves have the structure of shade leaves, whereas the upper leaves may be called sun leaves. While the xeromorphic upper leaves have more stomata per unit area, the size of the aperture is less. Correspondence is found between hair production and evaporation curves, both seasonally and in height above the soil. *Spiraea* is found to be less plastic, however, in respect to hairiness than are various plants previously reported (e.g. *Mentha aquatica* and *Polygonum amphibium*). It was found impossible to make the early leaves hairy or the later leaves smooth. The first parts to wither are those that are hairy. As to cause, hair production may be related to heredity, individual variation, or external factors. Of the latter it is believed that a diminished water supply is the most important. YAPP believes that *Spiraea Ulmaria* is becoming fixed as to the presence or absence of hairs; already the glabrous condition of the early leaves is a fixed character, and the hairiness of the later leaves is tending to become fixed. He concludes that xeromorphy is of physiological utility to those bog and marsh plants which exhibit it, but that no one factor can be singled out as of sole importance in determining xeromorphy. The physiological dryness of the soil is important, but it does not explain everything. For example, the presence of hygrophytic and xerophytic species side by side is likely to be explained by differences in transpiration, the xerophytic species generally being more exposed to severe transpiration.—H. C. COWLES.

Low temperature and plant tissues.—CHANDLER[5] has treated in considerable detail the killing of plant tissues by low temperature. He discusses the nature of injury by low temperature, giving a good summary of the literature relating to this subject. In his experiments he has shown that the killing temperature of many plant tissues may be reduced by means which increase the sap density; for example, intake of potassium chloride, glycerine, etc., or partial withholding of water. Rapidity of thawing had little effect on the amount of killing at a given temperature in case of all tissues experimented upon except that of ripe fruit of apple and pear. Previous exposures to low temperatures lowered the death point. In case of hardy winter buds and wood, a rapid fall of temperature increased the severity of injury. In fruit trees during early winter the wood at the base of the trunk and at the crotches of rapidly growing branches was found most susceptible to injury. At the stage of most complete maturity, the pith cells and fruit buds were most tender of all the above ground tissues. The hardiness of root tissue was found in general

[5] CHANDLER, W. H., The killing of plant tissues by low temperature. Research Bull. Agric. Exper. Sta. Univ. Mo. no. 8. pp. 143–309. *figs.* 3. 1913.

to vary indirectly with the distance from the crown. Roots of French crab, so extensively used in America as stock, are less hardy than roots from scions of an average variety of apple. It is of considerable interest to note that heavy dormant pruning, thinning of fruit, and application of nitrate fertilizers prolonged the growth period, lengthened the rest period, and consequently reduced the early forcing of growth in spring with subsequent injury by late frosts. The selection of trees with long rest period also helps to obviate the latter injury. Of apple blossom tissue, the pollen was found most resistant to low temperature.

The work presented in this bulletin is of such a character as to be of great interest alike to those engaged in "pure" science and to those whose chief interest is in the applied side.—L. I. KNIGHT.

Mitosis in Tetraspora.—In the green alga *Tetraspora lubrica*, MCALLISTER[6] finds that mitosis, so far as can be made out from the very small nuclei, corresponds in its essential features with that in higher plants. In the cell which is to give rise to 8 gametes, the resting nucleus contains a reticulum with net knots and a nucleolus. During the prophases, the reticulum develops chromatic bodies which apparently become arranged in a row to form a spirem thread. The nucleolus takes no part in this process. The spirem segments to about 13 chromosomes, which divide and pass to opposite poles. Details of spindle-formation were not made out, but there was found no reason to believe that *Tetraspora* differs from higher plants in this respect. Centrosomes or centrospheres, which might be expected on account of their reported presence in the gamete-forming cells of certain bryophytes, were not found. Cell-division is brought about by the splitting of a granular cell plate formed by the central spindle. The splitting takes place from the center outward.

The second and third mitoses follow quickly, but in each case the daughter nuclei enter the resting stage. The single pyrenoid of the original cell remains unchanged through the three divisions, so that it comes to lie in only one of the 8 gamete cells. In each of the other 7 cells one appears to arise *de novo* from the cytoplasm. The entire pyrenoid is said to fragment to form several starch bodies.

Since *Tetraspora* and other green algae resemble higher plants so closely in mitosis and differ so widely from the Euglenidae, the theory that the Chlamydomonadaceae, to which *Tetraspora* is held to be so closely related, have arisen from the Euglenidae is believed by MCALLISTER to be excluded.—L. W. SHARP.

Mitosis in Preissia.—In many papers dealing with mitosis in liverworts, attention has been focused chiefly upon the centrosome and related structures.

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[6] MCALLISTER, F., Nuclear division in *Tetraspora lubrica*. Ann. Botany **27**: 681–697. *pl. 56*. 1913.

In a study of *Preissia commutata*, Miss Graham[7] has emphasized the behavior of the chromatin. In the vegetative cells of the gametophyte, the earliest prophase is marked by an elongation of the nucleus and the appearance of large chromatin masses on the linin strands. These strands thicken, forming a spirem upon which the chromatin is borne in the form of chromomeres. The spirem shows a temporary contraction, after which it segments to form 8 chromosomes. The disappearance of the nucleolus is sudden and coincident with the appearance of the central spindle fibers, which suggests a material relationship between these structures. At telophase the chromosomes elongate to slender threads which lose their individuality in the reticulum of the daughter nuclei.

In the spore mother cell the reticulum gives rise to a leptonema spirem. Many threads lie side by side, but whether this represents a parallel conjugation or is without special meaning was not determined. Synizesis ensues. After the knot loosens up, the spirem thickens and for a time the chromomeres become more prominent. During a second contraction the spirem splits longitudinally and soon segments to form the bivalent chromosomes. The further behavior presents no unusual features.

In both somatic and heterotypic prophases there are hyaline caps at the poles of the nucleus, and in them, at least in the former case, the spindle fibers are formed. Centrosomes or centrospheres were not found at any stage.—L. W. SHARP.

Plant breeding in Sweden.—On account of the important practical results obtained at the Svälof Institute, as well as because of contributions to the science of heredity resulting from the extensive and exact investigations carried on at this station, an authentic account of its history, ideals, and methods coming from an authoritative source is especially welcome. The present director, NILSSON,[8] sketches briefly the origin of the organization, emphasizing the object, which was to arrive at absolutely practical results, and giving in some detail the sources of its income. In the development of methods, attention is directed to the comparatively small results coming from "selection in mass" as practiced up to 1891, when "pedigree culture" was introduced. Thus the method of isolating and studying pure lines derived from a single individual was practiced at the Svälof station for ten years before it was advocated by DE VRIES in his *Die Mutationstheorie* in 1901. With the adoption of this radically new method, results have been more abundant. NILSSON emphasizes the fact that the isolation of elementary species is only a preparatory auxiliary for getting out properly the material to be utilized, the essential thing being testing the practical value of the material and making the best selections. To

[7] GRAHAM, MARGARET, Studies in nuclear division of *Preissia commutata*. Ann. Botany **27**:661–681. *pls. 54, 55*. 1913.

[8] NILSSON, H. HJALMAR, Plant breeding in Sweden. Jour. Hered. **5**:281–296. 1914.

accomplish this specialists have been allowed to concentrate their attention on a limited field of one or two cereals. The importance of practical trials, the use of hybridization, and some of the practical results are noted, as well as the fact that mutations do appear in cultivated plants; but the main point of the paper is the contribution made to the science of plant breeding by the method of pedigree culture originated at the Svälof station.—GEO. D. FULLER.

The case of Oenothera.—Probably no genus of plants has ever been the subject and the cause of so much investigation as *Oenothera*. It has become a storm center, and it is to be hoped that the result will be the clearing of an atmosphere which has become heavy with discussion. The latest contribution to this field of controversy is by SHULL,[9] who suggests that *Oenothera* itself may be the occasion of the trouble, since "fundamental difficulties are encountered whenever attempts are made to apply to the Oenotheras rules of genetic behavior which are readily demonstrated in other groups of organisms." He concludes, for example, that *Oenothera* must have a hereditary mechanism fundamentally different from that which distributes the Mendelian unit characters.

In connection with the results of breeding experiments reported on in the present contribution, SHULL is convinced that certain conclusions reached by GATES regarding the origin and genetic nature of the *rubricalyx* character are erroneous, a character which the former has found behaving in various perplexing ways. The conclusions objected to are that the character represents a purely quantitative difference from *O. rubrinervis;* that it differs from the latter species in a single monohybrid Mendelian unit; and that the nature of a character itself, instead of the nature of the inheriting-mechanism to which it is related, determines the manner of inheritance of that character.—J. M. C.

Chromosomes and sex.—DONCASTER[10] has continued his breeding experiments in the study of sex-inheritance in the currant moth. In a previous paper he had described a strain which in each generation produced females only and showed that the oogonia of this strain had 55 chromosomes instead of 56, the normal number in the species. The more recent studies confirm the results previously announced and add further interesting data. It is found that the tendency to produce only females "varies in intensity," ranging from equality of the sexes to complete absence of males. It was discovered that the eggs of females with 55 chromosomes in the oogonia have 28 in one polar equatorial plate and 27 in the other. The facts as a whole make it clear that eggs which eliminate the 28th chromosome produce females, while those which

[9] SHULL, GEORGE HARRISON, A peculiar negative correlation in *Oenothera* hybrids. Jour. Genetics 4:83–102. *pls. 5, 6.* 1914.

[10] DONCASTER, L., On the relations between chromosomes, sex-limited transmission, and sex-determination in *Abraxas grossulariata.* Jour. Genetics 4:1–21. *pls. 1–3.* 1914.

retain it produce males. The author calls attention to the fact that this condition is "the converse of that described in most other insects."

The problem of the relation of chromosomes to sex-inheritance naturally becomes more complex as the facts accumulate, and the rather definite results obtained from the study of a few forms must be checked by the more general situation.—J. M. C.

Immunity as a physiological test.—VAVILOV[11] has suggested an interesting application of the specific relation that so often exists between a parasitic fungus and its host. He concludes that it has been demonstrated that immunity does not depend upon the anatomical peculiarities of plants, but upon their physiological peculiarities. Of course there is every evidence that in many cases there is some specific relation between a parasitic fungus and the metabolism of its host. The author suggests that "narrowly specialized" fungi may be used as a physiological test for the recognition of the species and races "in systematic and genetic studies of plants." He illustrates the possibilities in connection with a classification of the races of cereals, claiming that in this way he has been able to detect unsuspected races of wheat and oats. This coupling of the reactions of parasitic fungi with the genetic relationships of their hosts will be more of a promise than a performance until more exact knowledge has developed as to the metabolism of the fungi and of the hosts they are able to infect.—J. M. C.

A Welsh sand dune area.—Sand dunes historically interesting on account of their position over the site of the castle and buried city of Kenfig have been studied ecologically by ORR,[12] who has just made a preliminary report of the conditions and development of the principal plant associations. The area fringes the Glamorgan coast for 15 miles from Swansea. The pioneer association is, as usual, one of the Marram grass, followed by *Salix repens*. The efficiency of *Ammophila arenaria* as a sand binder seems to have been recognized here as early as 1330, when Kenfig made provisions for its protection and preservation. Upon the fixed dunes the final stage in the succession seems to be an association dominated by *Pteris aquilina* covering considerable areas. A more exact analysis of the factors concerned and a careful delimitation of the associations is promised in a future paper.—GEO. D. FULLER.

Cordaitean wood from the Devonian.—Miss ELKINS and Dr. WIELAND[13] have described wood of Cordaitales from the black shale of Indiana. The specimens from which the sections were made rested on black shale, and were large

[11] VAVILOV, N. I., Immunity to fungous diseases as a physiological test in genetics and systematics, exemplified in cereals. Jour. Genetics 4:49–65. 1914.

[12] ORR, M. Y., Kenfig burrows; an ecological study. Trans. Bot. Soc. Edinburgh 26:79–88. 1913.

[13] ELKINS, M. G., and WIELAND, G. R., Cordaitean wood from the Indiana black shale. Amer. Jour. Sci. 38:65–78. *pls. 1, 2. figs. 11.* 1914.

trees, all of them being silicified. The species described is called *Callixylon Owenii*, a genus recently established by ZALESSKY. Formerly it would have been called *Cordaites*, the new species being closely related to *Cordaites Newberryi*. The details of structure are very complete, and are perhaps more numerous and definite than have been obtained from any Devonian wood heretofore. What WIELAND calls its "advanced structural type" indicates great antiquity for the coniferophyte phylum.—J. M. C.

Some new Chlorophyceae.—TRANSEAU[14] has published some new species of green algae discovered in connection with his study of the periodicity of occurrence and reproduction of the algae of eastern Illinois. Thirteen new species are described in the following genera: *Zygnema* (1), *Spirogyra* (7), *Mougeotia* (1), and *Oedogonium* (4). In *Spirogyra*, 5 new varieties are also described. This is probably an illustration of the additional species of algae that will be discovered in connection with any intensive study of a region.—J. M. C.

Plants of Ohio.—SCHAFFNER[15] has published a catalogue of the vascular plants of Ohio, based on specimens in the state herbarium of the Ohio State University. The catalogue enumerates 2065 species, not including varieties, about one-fourth of which are introduced. The last preceding catalogue of Ohio plants was published by KELLERMAN in 1899. The present catalogue is really a check list of the collection of Ohio plants at the State University, and the serial numbers are the record numbers of the material.—J. M. C.

New plants from Mexico.—BRANDEGEE[16] has published a sixth fascicle of new Mexican plants collected by PURPUS, included in collections made chiefly in Chiapas in 1913. The following new genera are described: *Allophyton* and *Amalophyllon* (Scrophulariaceae), *Otocalyx*, *Plocaniophyllon*, *Stylosiphonia*, and *Pinarophyllon* (Rubiaceae), *Pterosicyos* (Cucurbitaceae), and *Tonalanthus* (Heliantheae). In addition to these new genera, 66 new species are described, distributed among 51 genera.—J. M. C.

The orchids of Java.—In presenting the fourth instalment of his studies of orchids of Java, SMITH[17] describes 48 species, included in 25 genera, 13 species being new. A new genus (*Abdominea*) is described, the excuse for the name being that the rostellum resembles the abdomen of an insect. The study of tropical vegetation is making large additions to our taxonomic lists.—J. M. C.

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[14] TRANSEAU, E. N., New species of green algae. Amer. Jour. Bot. 1:289–301. *pls. 25–29*. 1914.

[15] SCHAFFNER, J. H., Catalog of Ohio vascular plants. Ohio State Univ. Bull. 18:131–247. 1914.

[16] BRANDEGEE, T. S., Plantae Mexicanae Purpusianae, VI. Univ. Calif. Publ. Bot. 6:51–77. 1914.

[17] SMITH, J. J., Die Orchideen von Java. Bull. Jard. Bot. Buitenzorg II. no. 14. pp. 56. 1914.